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Influence of Sex and Body Mass on Harbor Seal (Phoca vitulina) Diving Behavior

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Influence of sex and body mass on harbor seal (*Phoca vitulina*) diving behavior

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MASTER'S THESIS

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A. Sasha McFarland

May 15, 2013

INFLUENCE OF SEX AND BODY MASS ON HARBOR SEAL (*PHOCA VITULINA*) DIVING BEHAVIOR

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Presented to
The Faculty of
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In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

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Abstract

The oceans are under increasing stress, both anthropogenic and natural. In the inland waters of Washington State, several fish species are showing depressed numbers. The harbor seal (*Phoca vitulina*), a piscivore, is the only year-round resident pinniped in the San Juan Islands. The numbers of this species have increased dramatically since the end of the bounty hunt in Washington State in 1960; however, the potential impacts of this predator on fish stocks are unknown. To predict population trends in prey fish stocks, we first must understand how they interact with their predators. Predators have energetic needs that vary with sex and body mass, potentially leading to different prey choice and consumption rates and, hence, to declines of targeted fish stocks. Harbor seals are an abundant, monomorphic predator, and their diving behavior can help us determine how sex, body mass, or both might use their habitat, and thus influence prey populations. I examined the diving behavior of adult harbor seals captured from the San Juan Islands, Padilla Bay, and Hood Canal, Washington, by comparing five variables summed or averaged per week: average maximal dive depth, total dive duration, total number of dives, total number of diving bouts, and Dive-profile Index (DPI; this variable is derived from the dive profile using an image analysis tool, and represents dive depth and dive duration). All five variables were tested using linear mixed-effects models to determine differences in the effects of body mass (small, medium or large) and/or sex (pregnant females, non-pregnant females, and males) while accounting for the random effects of haul-out site, date (week number) and individual seal. Comparisons were conducted during the pre- (April 5–July 5) and the post- (July 5–October 3) pupping seasons of 2002 and 2005 in Hood Canal, and 2007 and 2008 at Bird

Rocks and Padilla Bay. Body mass influenced several dive variables: larger seals dived significantly deeper than smaller seals during the pre-pupping season and for significantly longer durations during the post-pupping; they also had a significantly higher DPI than smaller seals during both seasons. Sex however had no effect on any dive variable. Deeper dives, longer dive durations, and higher DPI suggest that larger seals may have a greater negative impact on their targeted prey stocks than do smaller ones. When coupled with data on size distribution and bioenergetics models for harbor seals in the study area, the results of this study can help in assessing the impacts of this species on fish stocks.

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Introduction

The world's oceans are under increasing anthropogenic stress from many factors, including overfishing (Lubchenco et al. 2003). The rapid degradation of the oceans is drawing attention to the need for efficient and effective management practices to protect, rehabilitate, and maintain resources that are exploited by humans, such as commercial fish species, and natural predators alike (Allison et al. 1998). Worldwide, it is estimated that only 32% of individual commercial fish stocks are under-exploited or moderately-exploited, with the remaining 68% ranging from fully-exploited to depleted (Botsford et al. 1997). Of the depleted stocks, 23% are being fished below their Maximum Sustainable Yield (MSY), and 10% are being fished below half of their MSY (Neubauer et al. 2013). A total of 82 species of marine fishes are in danger of extinction in North American waters, with the population of large predatory fishes reduced by 90% (Musick et al. 2000a, Pauly and Watson 2003). The threat of extinction of marine fishes is increasingly urgent, and the implementation of scientifically-designed management plans is necessary (Musick et al. 2000b).

Another factor stressing fish populations is climate change. Climate change has been associated with changes in habitat, including shifts in temperature, circulation, stratification, nutrient input, oxygen content, and pH, leading to acidification (Doney et al. 2012). These oceanographic shifts cause population-level shifts due to organisms' intolerances of new environmental factors, changes in dispersal patterns of nutrients and plankton, and changes in species interactions as latitudinal shifts of ocean life and nutrients occur (Doney et al. 2012). For instance, the California Current ecosystem is showing decreased numbers of benthic fish such as rockfish (*Sebastes* spp.), due to bottom-water hypoxia, which is caused

by changes in the physical environment like increased water temperatures, current shifts, and stratification (Doney et al. 2012). That ecosystem is also showing reduced salmon numbers, because increasing water temperatures are driving lipid-rich zooplankton out of the region, thus reducing the survivorship of juvenile salmonids (*Oncorhynchus* spp.; Doney et al. 2012).

Marine organisms are also faced with regional pressures, including over-fertilization of agriculture leading to eutrophication, coastal and benthic habitat degradation, aquaculture, and invasive species (Ruckelshaus and McClure 2007, Doney et al. 2012). Food webs are tightly interconnected, and if one component of the web is affected by anthropogenic or natural stressors, the predators and the prey both are impacted. To gain insight into effective management practices for replenishing depleted populations one should examine the ecosystems rather than focusing solely on one issue (Botsford et al. 1997, Pacunski and Palsson 2001). Predator/prey interactions and habitat condition and availability should be considered. As marine predators, pinnipeds have been implicated in stunting the recovery of overfished fish stocks; hence, understanding their role in the ecosystem is essential to fisheries management (Fu et al. 2001, Trzcinski et al. 2006).

Pinnipeds and Fisheries

The interaction between pinnipeds (seals, sea lions, fur seals and walruses) and fisheries has been a source of ongoing debate since the early 20th Century. As motorized boats became available for fishing, competition increased between humans and these marine mammals. In the early to mid-20th Century, bounty hunts were initiated in many places,

including North America and Europe, to cull pinniped populations. By the 1970s, some pinniped populations had declined to as low as 5% of historical levels and, consequently, hunting moratoria were put in place (Heide-Jørgensen and Härkönen 1988). Recently, the controversy over the impact of pinnipeds on commercial fish stocks has resumed due to a combination of fishing fleets moving inshore, where most pinnipeds are distributed, and pinniped populations rebounding (Harwood 1987).

Many pinnipeds are opportunistic generalist predators that consume whatever prey are available. Harbor seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are typically such predators, relying on prey that can vary by habitat or season. A pinniped living in an estuary will have access to different prey than those hauling out near pelagic waters, and different prey species may be present in the area in the spring than in the summer. Within the patterns of generalist predators, individuals may also target specific prey (Bromaghin et al. 2013). Specialist predators, such as walruses (*Odobenus rosmarus*), have the potential to deplete stocks more quickly than generalists, as they focus only on one prey as a species (Northridge and Beddington 1992). However, it has been suggested that although generalist predators do not consume enough of one species of fish to cause a dramatic decline in numbers, they do prevent the recovery of depleted stocks (Bax 1998). For the last decade, there has been an ongoing debate about the role of grey seals in the decline of the of Atlantic cod (*Gadus morhua*) populations in Eastern Canada. Scientists agree that they were not major contributors to the decline, but they may be contributing to the lack of recovery (Fu et al. 2001, Trzcinski et al. 2006). In the Gulf of St. Lawrence, predation by grey seals may have an impact on recovery (Chouinard et al. 2005), but along

the Scotian Shelf, Trzcinski et al. (2009) suggest that they are responsible for only 0.2% of natural mortality, and thus do not have significant impacts on recovery. In Europe, modeling of three river systems of different sizes in Scotland demonstrated that removing harbor seals from the rivers would increase the stock numbers of Atlantic salmon (*Salmo salar*) only in the smallest river, indicating that harbor seals are not major stressors in large rivers (Butler et al. 2006). Similarly, grey seals do not significantly impact the herring population in the North Baltic Sea (Gårdmark et al. 2012). Although the oldest age class of herring may be impacted by grey seals, the herring population seems to be increasing with the grey seal population (Gårdmark et al. 2012). It follows that the impact generalist predators have on fish stocks depends on more factors than simply the predator's needs, and include prey population numbers, habitat availability, and other habitat stressors.

In the inland waters of Washington, harbor seals are the most abundant marine mammal with a population of approximately 15,000 animals (Jeffries et al. 2003). They are the only pinniped species that breeds and resides year-round in Washington (Brown et al. 2002, Jeffries et al. 2003). Harbor seal numbers in the inland waters of Washington have fluctuated historically. During the 1940s and 1950s, a state-financed harbor seal bounty hunt was initiated to reduce harbor seal numbers in Washington. Between 1943 and 1960, approximately 17,133 harbor seals were killed (Newby 1973). The ending of the hunt in 1960, coupled with the passing of the Marine Mammal Protection Act in 1972, resulted in a steady increase in the number of harbor seals. Between 1978 and 1999, the harbor seal population in Washington (including the inland waters and the outer coast) increased three-fold, from 10,383 animals to 29,650 (Jeffries et al. 2003). Since 1999, the population has

remained steady at the carrying capacity for the region (Jeffries et al. 2003). Although the rate of increase is near zero, the population of harbor seals in Washington is high enough to potentially impact the recovery of depleted fish populations.

In the inland waters of Washington, 0.1% of invertebrates (3/3000), 13% of fishes (28/219), 18% of birds (23/128), and 45% of mammals (9/20) are listed as a species of concern either federally in the U.S. or Canada, or by the State of Washington or the Province of British Columbia (Gaydos and Brown 2009). Fish listed as species of concern in the region include 14 species of rockfish, eulachon (*Thaleichthys pacificus*), Pacific cod (*Gadus macrocephalus*), Pacific hake (*Merluccius productus*), Pacific herring (*Clupea harengus pallasi*), seven stocks of five salmonids (including the steelhead trout, *O. mykiss*), the bluntnose sixgill shark (*Hexanchus griseus*), the shortspine thornyhead (*Sebastolobus alascanus*), the bull trout (*Salvelinus confluentus*), and the walleye pollock (*Theragra chalcogramma*; Gaydos and Brown 2009). Harbor seals are opportunistic marine predators that prey on locally- and seasonally-abundant fish and invertebrates (Lance et al. 2012). Along with California sea lions (*Zalophus californianus*), they are considered major stressors on stocks of Pacific herring, and potential inhibitors of the recovery of Pacific hake, walleye pollock, Pacific cod, and demersal rockfish stocks (West 1997). Fatty acid analysis has revealed that up to 50% of the diets of some individual harbor seals living in the inland waters of Washington are composed of Black (*S. melanops*) and Yellowtail (*S. flavidus*) rockfish (Bromaghin et al. 2013). Scat analyses showed Pacific herring and Pacific sand lance (*Ammodytes hexapterus*) were the most common year-round prey, with salmon

being prevalent in summer and fall (Lance et al. 2012). For species with depressed population numbers, those amounts of predation may be crippling.

To understand potential detrimental impacts of pinnipeds on prey populations, we need to understand foraging behavior, which can be influenced by many factors. Energetic requirements, determined by age, body mass, and/or sex can contribute to foraging needs. Although body mass and sex may be linked in influencing diving behavior, the two have largely been investigated in size-dimorphic species, by sex or body mass independently, or by pairing sex with age rather than body size (Thompson et al. 1989, Le Boeuf and Laws 1994, Coltman et al. 1997, Härkönen et al. 1999, Härkönen et al. 2001, Frost et al. 2001, Baechler et al. 2002, Beck et al. 2003a, b, Hastings et al. 2004). I chose to examine the effect of body size and sex on the foraging behavior of a relatively size-monomorphic species, the harbor seal. To exclude the confounding effect of age, I focused on the diving behavior of adult seals.

The Influence of Body Mass on Foraging Behavior

In general, energetic needs are higher for larger animals, and therefore they require a higher calorie diet (Klieber 1961). Hence, other factors being equal, large animals must either be more efficient foragers, or they must be adapted to spend a higher percentage of time foraging than small animals. There is evidence supporting both possibilities. Behavior of large herbivores, grey seals, fur seals, and walruses, all of which are size-dimorphic, support the hypothesis that larger animals are more efficient foragers (Mysterud 2000, Schreer et al. 2001, Beck et al. 2003b). This efficiency may be explained by the gut-size

hypothesis, the prey-size hypothesis, or by differences in prey capture ability. Large animals with large gut size can digest prey of low quality, therefore are less selective, resulting in a decrease in foraging effort because the animals do not have to search as extensively for suitable prey (Beck et al. 2003b). Also, larger animals can eat larger prey, satiating more quickly, thereby reducing time searching for prey (Beck et al. 2003b).

Another possibility to explain dive differences is that small animals may be physiologically limited in their diving abilities. Schreer et al. (2001) supported this theory by showing that dive duration in birds and true seals was the limiting factor for smaller animals. Larger animals were able to dive deeper and for longer than smaller ones. Dive duration scales to body size in Antarctic pinnipeds and seabirds, and in cetaceans (Boyd and Croxall 1996, Noren and Williams 2000), because the larger of those species are physiologically adapted to spend more time diving. For comparison, in humans, the total oxygen store is 20 ml O_2/kg, whereas in elephant seals it is 100 ml O_2/kg (Kooyman 2002). In terrestrial animals, the lung is an important component in oxygen stores, but in marine mammals, the blood and muscles store the oxygen (Kooyman 2002). Marine mammal blood volume is 1.5 times that in humans, hemoglobin concentration is three times that in humans, and myoglobin concentration is approximately ten times that in humans (Kooyman 2002). Marine mammals with greater mass can remain submerged for longer periods without pausing to re-oxygenate.

Additionally, marine mammals have a dive reflex that induces bradycardia, body temperature decrease, and peripheral vasoconstriction (Hill et al. 1987). When activated, the reflex allows them to efficiently use blood and muscle oxygen stores, which in turn

maximizes diving efficiency. In Weddell seals, the intensity of the dive response varies inversely with the level of metabolism being used by their muscles (Davis and Williams 2012). Weddell seals demonstrated a combination of dive response and exercise response. When the animals were not exerting themselves, the dive response was strong (and heart rate was low), but when they were exerting themselves, the dive response was weaker: as stroke frequency increased, heart rate increased (Davis and Williams 2012). The top 30 m of the dive were excluded in this study, because on the descent, tachycardia from the surface period was still apparent, and on the ascent, the seals were coming out of the dive reflex. In dives below 50 m, the stroke frequency and heart rate both decreased as the seals spent more time gliding rather than stroking. Greater depths allowed for more gliding, in turn maximizing oxygen stores and allowing for greater dive durations (Davis and Williams 2012).

The Influence of Sex on Foraging Behavior

Energetic needs of pinnipeds, and thus potentially foraging behavior, are different for males and females depending on activity and life stage (pregnant versus non-pregnant, pupping, molting, breeding; Beck et al. 2003a). Males and females, particularly in size-dimorphic species, exhibit different foraging behavior, including depths of dives, duration of foraging trips, and distances from the haul-out during foraging trips. Three hypotheses have been advanced to explain differences in foraging behavior by sex: sexual dimorphism, reduced intersexual competition for food, or energetic costs of reproduction/reproductive strategy (Beck et al. 2003b). The sexual-dimorphism hypothesis suggests that, because

metabolic requirements increase with body size, the large sex requires more energy per unit time than the small sex. The reduced-intersexual-competition hypothesis suggests that males and females forage in different locations and on different prey to reduce competition, as observed in ungulates (Main et al. 1996). Data to support this second hypothesis are difficult to collect in any season, and nearly impossible to collect during the reproductive season, as discriminating between reduced intersexual competition and reproductive strategy is very difficult. The energetic-costs-of-reproduction/reproductive strategy hypothesis suggests that reproductive success is determined by different factors for males versus females. For males, strength and endurance increase the likelihood of success by increasing access to as many mates as possible, although matings are still possible for small animals (Beck et al. 2003b). The costs of gestation and lactation for females, however, are higher than those of mate-acquisition for males (Beck et al. 2003b).

Studies on sex and size in pinnipeds have focused on sexually dimorphic species (Le Boeuf et al. 2000, Winship et al. 2002, Beck et al. 2003a, b, Call and Ream 2012). At Sable Island, Canada, grey seal behavior supports the energetic-costs-of-reproduction/reproductive strategy hypothesis (Beck et al. 2003a). Leading up to the breeding season in the fall, males maximize growth and formation of energy reserves by taking longer, deeper dives than the ones they perform during the non-breeding season (though not as long or as deep as the dives of females). Small body size may reduce the chance of matings for males, but the impact of reduced body mass is not as great for males as for females. Female reproductive success is defined by survival of offspring, which is directly related to her body condition. Her behavior demonstrates efforts to reduce risk to offspring during the lactation period,

including taking shorter, shallower dives, and staying close to the haul-out so as not to expose her offspring to excessive risk of predation or exhaustion. The behavior of females also reflects efforts to gain energy needed for raising and weaning healthy offspring during the summer, including increasing foraging time and depth leading up to the pupping season (Beck et al. 2003a). During the post-molting season, males do not immediately replenish fat reserves, as there is little advantage to carrying extra weight and blubber through non-reproductive seasons (Beck et al. 2003a). In contrast, the more quickly females regain good body condition post-molt, the earlier implantation will occur. Early implantation leads to whelping a larger pup, which increases likelihood of survival for that pup (Beck et al. 2003a). During low prey abundance years, females of the size-dimorphic Antarctic fur seals increased their dive durations and diving activity, whereas males did not (Boyd et al. 1994). Females showed a 30-50% increase in cost of foraging over abundant prey years (Boyd et al. 1994).

We know little about monomorphic species, and therefore cannot discern whether differences in behavior are sex- or body mass-related. Harbor seals are slightly size-dimorphic but do not exhibit any other sexual dimorphism (e.g., pelage patterns or cranial structure). Male harbor seals reach a maximal length of 190 cm and weight of 170 kg, 12% longer and 31% heavier than females, which reach a maximal length of 170 cm and weight of 130 kg (Reeves et al. 2002). Male grey seals, by contrast, reach a maximum of 260 cm and 350 kg, which is 30% longer and 75% heavier than females, which grow to 200 cm and 200 kg (Reeves et al. 2002). Even more dramatically, male Steller sea lions (*Eumetopias jubatus*) grow to 330 cm and 1,100 kg, 14% longer and 214% heavier than females, which

reach 290 cm and 350 kg (Reeves et al. 2002). The size differences in harbor seals are considered too small to classify them as dimorphic (Riedman 1990).

Studies on harbor seals have focused on the effects of sex and age on haul-out use and horizontal movements, not on sex and/or body mass on diving behavior. In the Skaggerak, off the coast of Sweden, young females spend more time foraging when nursing a pup than old females, resulting in increased pup mortality (Härkönen et al. 1999). In Alaska, juvenile seals move further from their haul-out sites than adults, and both juvenile and adult females have larger home ranges than males throughout the winter and fall (Lowry et al. 2001). Foraging trips of male harbor seals in Scotland are longer and more extensive than those of females, with large intrasexual variation and a distinct positive trend between body mass and proportion of time spent at sea (Thompson et al. 1998). Dive shape (e.g., v-shaped with little bottom time, u-shaped with long bottom time) varies in Nova Scotia relative to age and sex (Baechler et al. 2002). Females in Alaska exhibit less focused diving (they spend time diving to each of six depth categories rather than only diving to one) than males, but the effect of body mass was not tested (Frost et al. 2001, Hastings et al. 2001).

In this study, I investigated the relative influence of body mass and sex on the diving behavior of harbor seals in the inland waters of Washington State. I examined five dive-related variables by sex and body mass at three haul-out sites in the inland waters of Washington: a rocky reef, a muddy intertidal bay, and a protected fjord, and relative to two seasons: pre-pupping and post-pupping. Due to sample size limitations, I did not test for seasonal differences; rather I divided the data into the two seasons and tested them

independently of one another. If sex alone were important, large and small males would behave similarly to one another as would large and small females, supporting the-cost-of-reproduction/reproductive-strategy hypothesis. If body mass alone were important, large males and females would behave more similarly to one another, as would small males and females, supporting the-large-body-size-equals-larger-energetic-needs hypothesis. If the interaction of sex and body mass were important, large males, small males, large females, and small females would all behave differently, or certain aspects would be similar while others were different, supporting both hypotheses. For instance, small males and females may both dive shallowly for short periods of time, large males may dive deep for long periods of time, and large females may dive shallowly for long periods of time.

Methods

Study Area

I collected and analyzed data from two study sites, Bird Rocks and Padilla Bay, and analyzed previously-collected data from Bird Rocks, Padilla Bay, and Hood Canal. Data from Bird Rocks and Padilla Bay were collected during 2006–2007 with the help of colleagues at Western Washington University, and data from Hood Canal were collected during 2002 and 2005 by collaborators at Washington Department of Fish and Wildlife (WDFW). The two northern sites were chosen because of their accessibility and because of the contrast in habitat immediately available to the animals. The Hood Canal site was

included because comparable data were available from that site, which provided a higher sample size and a third type of habitat.

Bird Rocks is a rocky-reef haul-out site located in Rosario Strait on the eastern end of the San Juan Island Archipelago (48°29’09”N, 122°45’44”W; Figure 1). Water depths surrounding this haul-out rapidly descend to over 150 m, and the deep waters of the Strait of Juan de Fuca are also readily accessible. This haul-out is accessible to harbor seals both at high tide and low tide.

Approximately 10 km east of Bird Rocks is Padilla Bay, an estuarine tidal mudflat haul-out located at the mouth of the Skagit River (harbor seal mudflat haul-out at 48°29’07”N, 122°31’41”W; Figure 1). The bay is ~42 km^2 in area with a maximal depth at mean lower low water of 8 m. This bay is unique in many ways. Fresh water is deposited via small sloughs and two river estuaries. At low tide, shallow channels with muddy banks are exposed, providing haul-out sites for harbor seals; at high tide, the haul-out sites are underwater. Additionally, eelgrass (*Zostera marina*) covers 70% of the bottom (Bulthuis 1995), providing an important habitat for young fish and spawning Pacific herring (Penttila 2007). Because of its unique habitat characteristics, Padilla Bay is classified as a National Estuarine Research Reserve.

Approximately 140 km to the south of the San Juan Islands is Hood Canal, a fjord-like water body located on the Olympic Peninsula that exchanges sea water only with Puget Sound. The harbor seal haul-outs are located along the banks of the Dosewallips River (47°41’23 ”N, 122°53’39”W), the Duckabush River (47°39’04”N, 122°55’52”W), and Fulton Creek (47°37’05”N, 122°58’30”W; Figure 1), near their confluences with Hood

Canal. Hood Canal is a deep, glacially-carved body of water that has a glacial moraine at its mouth limiting the flow of water and nutrients in and out of the canal (Simonds et al. 2008).

Harbor seal population estimates in my northern study areas follow trends recorded for the Washington population. The total population estimate for the San Juan Islands and Eastern Bays increased from 2,459 in 1978 to 8,356 in 1999, and in 2007 was holding steady at 8,121 animals (Jeffries et al. 2003, Hardee 2008). Hood Canal population numbers showed no growth between 1978 and 1999 (1,120 and 1,088, respectively; Jeffries et al. 2003). All these numbers are near carrying capacity for all the study areas (Jeffries et al. 2003).

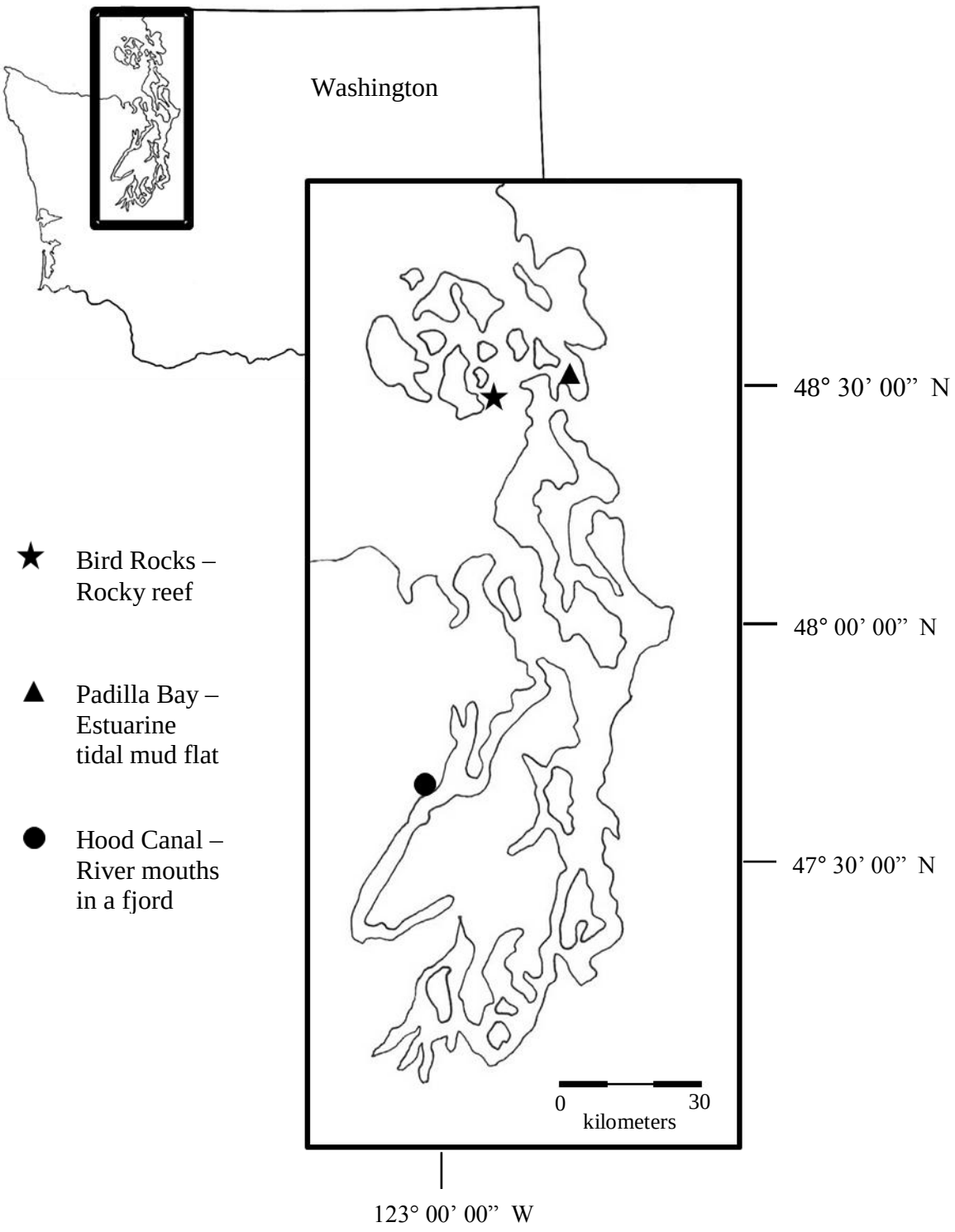


Figure 1. Study area in the inland waters of Washington. Symbols indicate the three tagging sites: rocky reef, estuarine bay, and river mouths in a fjord.

Data Collection – Tagging

Research for this study was approved by the Institutional Animal Care and Use Committee at Western Washington University (Protocol Number 06-005), and was conducted under the Marine Mammal Protection Act Scientific Research Permit 782–1702 issued to the National Marine Mammal Laboratory by NOAA's Protected Resources Division. Harbor seals were captured by biologists from WDFW with the assistance of Western Washington University students, following the methods of Jeffries et al. (1993). Seals from Bird Rocks were caught in 2006 and 2007 using salmon nets by quietly approaching hauled-out animals and trapping them under the net. Seals tagged at the Padilla Bay site were caught in 2006 and 2007 using a beach-seine method, in which researchers laid out a net and rushed a beach haul-out from the water. The seals were caught in the net as they entered the water. Seals from both Bird Rocks and Padilla Bay were then transferred to sturdier hoop nets for a short transport to a processing site, where they were weighed, measured, and flipper-tagged for ID purposes. Blood and blubber samples were collected, ultrasounds were performed on females to determine pregnancy, and the general health of the animals was assessed to determine if the animal was a suitable candidate for instrument attachment. The animals were tagged with time-depth recorders (TDRs; used for this study) and satellite tags (used for concurrent studies). A similar capture and tagging process was carried out in Hood Canal by our collaborators at WDFW in 2002 and 2005.

The TDRs used in this study were Mk-9s (TDR only) and Mk-10s (TDR and Wildtrack Telemetry Fastloc GPS, which can acquire GPS fixes while archiving TDR data) from Wildlife Computers, Redmond, WA. Both tags collected the same dive data. TDRs

were programmed to record time, pressure (depth), light level, wet/dry conditions, and temperature every 10 s for the duration of battery life (which should have exceeded deployment time). TDRs were glued along the dorsal midline between the shoulders using 5-min epoxy glued directly to the pelage. Tags were designed to remain attached until the fall molt, at which time the glued hair would be shed along with the tags. TDRs were equipped with an Eco-tech flotation pack with VHF transmitter to allow for tag retrieval. Flotation packs were designed to float with the antenna above-water for post-molt recovery of floating tags.

Tagged seals were tracked via satellite telemetry using the Argos Satellite system and boat-based radio telemetry using a 19-ft inflatable boat. VHF tracking was intended to ground-truth the satellite data, to assess the condition of tags and tagged animals, and to retrieve tags once they fell from each seal.

Data processing

In the inland waters of Washington, 45.1% of all harbor seal dives are presumed to be foraging dives (based on the presence of vertical up and down movements, or "wiggles" associated with prey pursuit). 35.5% of dives are equally divided between short and shallow, and long and deep non-foraging dives, and 19.4% are equally divided between left- and right-skewed v-shaped dives, both of which may be for foraging or travel. Thus, although not all diving is for foraging purposes, a majority of dives are likely driven by differences in prey availability.

Dive data were processed using Wildlife Computers Dive Analysis software (v. 1.0.55). Dive profiles were corrected to account for drift in the depth sensor throughout the deployment. Typically, dive start depths are set at twice the resolution of the tag (Baechler 2002, Reuland 2008). Mk-9 and Mk-10 tags have a depth resolution of 0.5 m and are accurate to ±1% of the reading; therefore, dives could begin at 1 m depth. To account for the shallow depths of Padilla Bay while being conservative about surface noise, I set the dive start depth at 2 m. This start depth increased the average number of dives compared to the standard 5-m start depth of other studies by 26% (from 18,205 to 22,958) at Bird Rocks, 27% (from 10,057 to 12,774) in Hood Canal and 212% (from 8,797 to 27,482) in Padilla Bay, demonstrating that a large number of dives would be lost (particularly for Padilla Bay seals) if a 5-m start depth was used.

I used five variables to describe dive behavior and hence foraging behavior (Beck et al. 2003b): average maximal dive depth (depth), total duration of time spent diving (duration), total number of dives (# of dives), total number of bouts (# of bouts), and Dive-profile Index (see below). TDR datasets recorded over a prolonged period of time are overwhelmingly large. Every dive a seal takes is recorded as a datum. A seal with a 9-month deployment, for instance, can have as many as 30,000 dives in its profile. Furthermore, each dive is highly correlated with the previous dive, and the number of data points per seal makes comparisons between variables without violating statistical assumptions very complicated, if not impossible. To reduce the dataset and limit autocorrelation, I summarized all variables into one-week time periods. I chose one-week periods because it

provided a manageable data set without averaging away the variability, as would have been the case if I had summarized my variables into one datum per month or season.

Dive depth is largely a factor of prey distribution (McCafferty et al. 1998, Beck et al. 2007, Grigg et al. 2012, Jaud et al. 2012). Depths are determined by local bathymetry, efficiency as predators (they are less efficient at shallow and deep depths), costs and benefits of feeding on different prey, and prey availability, both vertically in the water column and spatially (Härkönen 1987, Tollit et al. 1998).

Dive duration is limited by oxygen stores available to the individual (Schreer et al. 2001). Large animals have more myoglobin-rich skeletal muscle, physiologically allowing them to hold their breath longer. However, animals with the highest energetic needs are not always the largest animals, in which case benefits of longer dive durations may outweigh energetic costs of foraging for longer durations.

Number of dives per week indicates how an animal utilizes its time underwater. Animals can take a high number of dives with shorter duration and spend as much time foraging as an animal taking fewer dives with longer durations. Number of bouts similarly shows how individuals utilize their foraging time, for example by taking frequent short bouts or less frequent long bouts.

Dive profile index is a novel variable that combines dive depth, duration, number of dives, and number of bouts to represent the "area under the curve" of the "graph" that is the weekly dive profile of each animal (Figure 2). By comparing the amount of black in each week of each animal's dive profile, we capture a combination of four dive variables. The largest dive profile indices will be those of animals that dive frequently for longer durations

to deeper depths. The smallest dive profile indices will be those of animals that dive infrequently, shallowly, and for shorter durations. Intermediate dive profile indices represent animals in which dive frequency, depth, and duration are not all rather large or rather small. I calculated DPI using ImageJ (v. 1.42; National Institute of Health, Bethesda, MD) image analysis software. First, I created an image of each week of each seal's dive profile, which varied by seal and throughout the season for each individual (Figures 2a–c). The x-axis was standardized by date and time, and the y-axis, was standardized by depth. Once I created the images, I used the "Analyze Particles" tool in ImageJ to calculate the "amount of blue" (shown as gray in the figures) of the dive profile. The longer the seal spent at deeper depths, the larger the DPI of the profile. If one were to examine DPI on, say, a daily scale, factors such as descent time, bottom time, and ascent time would play a larger role.

Depth, duration, and # of dives were calculated directly using the output from each animal's tags. Depth was calculated using means (± SD) of each animal's dive depths for each week of their deployment period. Duration was the sum of each animal's dive durations for each week of his or her tag's deployment. Number of dives was a count of each animal's dives for each week of his or her tag's deployments.

Bouts were determined by combining the dives into bouts following the methods of Reuland (2008). Specifically, a bout began after a seal had been at the surface for at least 15 min and had completed at least four dives to a depth of >2 m with a surface interval of less than 1.5 min. A bout ended when a seal remained at the surface for longer than 1.5 min. Once bouts were determined, the sums of the total number of bouts per week of each animal's deployment were calculated.

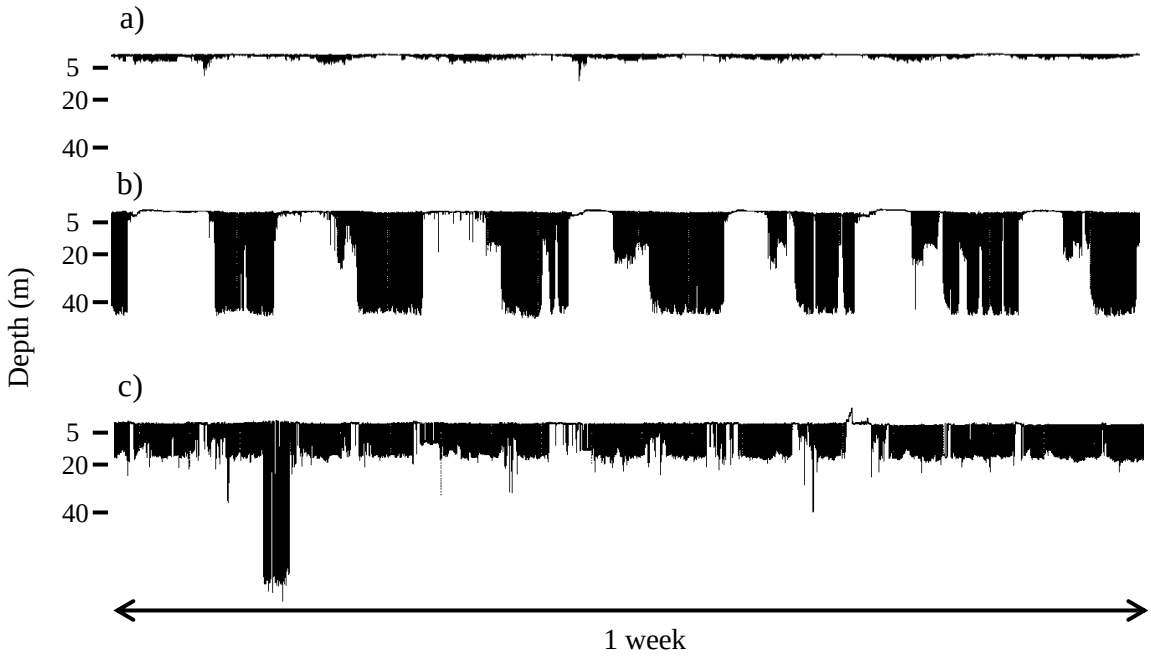


	Figure		
	a	b	c
DPI:	7510	85719	55478
Average depth (m):	3.5	40.0	21.0
Duration (min):	3666	6295	9099
# of dives per week:	1488	1654	2205
# of bouts per week:	194	64	84

Figure 2a-c. Snapshot of one week of a dive profile from each of three seals, as used to calculate DPI. Dive profile images show variation in weekly dive patterns, with a) a seal from Padilla Bay taking many short shallow bouts, b) a seal from Hood Canal taking few deep bouts, and c) a seal from Hood Canal taking an intermediate number of bouts to intermediate depths. Note how DPI reflects the image.

Data analysis

I standardized each seal's deployment period by week regardless of year of capture. I called 21 December (the shortest day of the year) the first day of Week 1, regardless of day of the week. Defining date by week number allowed me to align and compare seals' dive behavior on a biologically relevant scale, based on daylight rather than arbitrary days of the week. I then divided the study period into two seasons, also on because they are biologically relevant to the seals: pre-pupping and post-pupping. Energetic requirements during these two biologically important seasons are much different, so it was important to account for the energetic differences (Howard et al. 2013). In the San Juan Island sites, harbor seals pup around July 1st (Huber et al. 2001). Because I averaged my data per week, I set the week of July 5th as the beginning of the post-pupping season. Hood Canal seals, however, pup approximately six weeks later in mid-August (Jeffries et al. 2000). To allow for comparison between the two northern sites and the Hood Canal site, I moved the Hood Canal data forward six weeks so the week of August 16th (the beginning of the post-pupping season in Hood Canal) would align with the week of July 1st (the beginning of the post-pupping season of the other two sites).

I divided sex into three biologically relevant categories: males, pregnant females, and non-pregnant females. I divided females because I expected pregnant and non-pregnant females to exhibit different dive behaviors given the different metabolic needs of a female growing and nursing a pup versus one without those biological pressures (Howard et al. 2013). I divided body mass into three categories using the 33rd and 66th percentiles of all the seals in the study (small = 47–69.5 kg, medium = 69.5–91.5 kg, and large = 91.5–113.5 kg).

I used Linear Mixed Effects Models (LMEM) in R (v. 2.1.0) programming software to compare all five variables individually by sex and body mass during the pre-pupping and post-pupping seasons. Mixed effects models are designed to handle large, unbalanced data sets and repeated measures, and analyze clustered data, rather than independent and identically distributed data (Demidenko 2004, Pinheiro and Bates 2004). They distinguish two types of coefficients, within (population-averaged) and between (individual-specific) clusters to describe relationships between response variables and covariates in the data (Demidenko 2004, Pinheiro and Bates 2004). Mixed models treat the population-averaged coefficients as fixed effects, but treat the individual-specific coefficients as random effects (Pinheiro and Bates 2004).

I tested each of the five dive variables using sex, body mass, and their interaction as fixed effects, and date, haul-out site, and seal ID (a unique number assigned to each individual) as random effects. Date was included in the model because I expected that diving behavior would change, particularly for pregnant/post-partum females, leading up to pupping and after pupping. I expected females to be building energy stores by diving deep for long periods of time leading up to pupping, then to change to short, shallow dives after pupping. I expected males to be building energy reserves leading up to the breeding season (about four weeks after pupping in mid-summer, and prior to the molt in the fall), but then to alter their behavior during the breeding season.

Haul-out site was included because the habitats at all three haul-outs were different, including the substrate (e.g., rocky reef vs. mud), water depths (8 m at mean lower low water in Padilla Bay vs. 54 m in Hood Canal and 72 m in Rosario Strait), nutrient flux (e.g.,

high around the San Juan Islands, but low in Hood Canal, leading to eutrophication in the latter site), human activities (e.g., shipping lane in Rosario Strait vs. recreational boating activity in Hood Canal vs. refinery operations in Padilla Bay), and freshwater influx (from large rivers in Hood Canal and Padilla Bay). These habitat differences support different age groups and types of prey, which would logically affect diving behavior.

I determined the most informative model by including all possible combinations and choosing the model with the lowest Akaike Information Criterion (AIC) score (Demidenko 2004). If the model with the next lowest AIC score was a significantly better fit, I chose it instead (Pinheiro and Bates 2004). I repeated those methods for the random, then the fixed effects to determine the most parsimonious model. If significant differences were found by sex or body mass in my model, I ran a post-hoc pairwise t-test with a Bonferroni correction to determine where the differences occurred. All results are presented as mean ± SD.

Results

A total of 57 adult harbor seals (29 females and 28 males) were captured and tagged at the three haul-out sites: 15 at Bird Rocks (4 females and 11 males), 21 at Padilla Bay (15 females and 6 males), and 21 at the Hood Canal sites (10 females, 11 males). Of those, 38 tags were recovered from 19 adult males, 12 pregnant females, and 7 adult non-pregnant females (Table 1). Deployment start and end dates were staggered slightly, because we did not capture all seals on the same date, and tags were molted on varying dates. Thus, some figures show shortened start and end dates for deployments for different classes of seals

(Figures 5, 6, 9, 10, 13, 14, 17, 18, 21, and 22). Among these 38 seals, the average body mass of males was 83.8 ± 17.4 kg, approximately 18% higher than pregnant females, which averaged 70.9 ± 16.9 kg, and 31% higher than non-pregnant females, which averaged 63.8 ± 12.0 kg. The average length of males was 149 ± 8 cm, only 9% higher than pregnant females, which averaged 137 ± 10 cm, and 7% longer than non-pregnant females, which averaged 139 ± 7 cm. We recaptured one animal in both 2007 and 2008. In 2007, she was not pregnant when captured on April 19th, but in 2008 she was pregnant when captured on February 25th. She was 19 kg heavier in 2007, when she was not pregnant, than in 2008, when she was captured earlier in the season. Detailed capture data for all seals are provided in Appendix A.

Overall, results indicate an influence of body mass but not sex in the variables tested. Average maximal depth, average duration, and dive profile index were significantly influenced by body mass during at least one season. No variables were influenced by sex during either season. Number of dives per week and number of bouts per week were not significantly influenced by sex or body mass in any of the models tested. As with many marine mammal studies, my sample size, and therefore power, were low, potentially contributing to a lack of significant results. Although I initially tested for sex using three sex categories (non-pregnant females, pregnant females, and males), due to small sample size I also repeated the analyses using only two sex categories (females and males) and still found no significant influence of sex on any of the dive variables.

Results are presented by season, although season did not significantly influence any of my results. My data were categorized by season because it was a biologically relevant,

logical way to simplify and analyze my data. In some cases, differences were found during one season but not the other. This presentation of findings should not be misinterpreted to mean that there were significant differences by season; it only concludes that the particular variable was influenced during one season but not the other.

Narrative results follow for all of the significant findings, and figures and tables are included for all variables, significant or not. A summary table of results is at the end of this section (Table 12).

Table 1. Harbor seal capture data for animals for which tags were recovered.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	2	7
Pregnant	2	5	5	12
Male	6	3	10	19
Body mass				
Small (47-69.5 kg)	0	8	6	14
Medium (69.6-91.5 kg)	8	3	7	18
Large (91.6-113.5 kg)	1	1	4	6

Average Maximal Depth per Week

Average maximal depth per week was influenced by body mass, but not sex, during the pre-pupping season, but there were no significant results by either variable during the post-pupping season (Tables 2a–d and 3; Figures 3–6). Average weekly maximal depths for the pre- versus post-pupping seasons were similar for all sexes: males: 20 ± 12 m versus 20 ± 15 m; non-pregnant females: 12 ± 7 m versus 11 ± 8 m; and pregnant females: 15 ± 11 m versus 21 ± 15 m. None were significantly different (two-sample unequal variance t-test; $P > 0.05$ for all tests).

During the pre-pupping season, small seals did not dive as deep as medium or large seals, and no significant difference was found between medium and large seals. Small seals started the deployment period diving to approximately 50 m, then dived only to 10 m by May 10 for the duration of the pre-pupping season (Figure 6a). Medium seals dived to between 20 and 40 m throughout the pre-pupping season. Large seals initially dived steadily to 20 m, and then jumped between 20 and 40 m for the duration of the pre-pupping season.

Average depths for the pre- versus post-pupping by body mass were 8 ± 8 m versus 13 ± 11 m for small seals, 21 ± 11 m versus 24 ± 15 m for medium seals, and 22 ± 3 m versus 19 ± 7 m for large seals. None of these were significantly different (two-sample unequal variance t-test; $P > 0.05$).

Tables 2a–d. Pre-pupping average maximal depth sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold font.

Table 2a. Sample size for pre-pupping average maximal depth per week, by sex/status and body-mass attribute and location.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	0	5
Pregnant	2	5	1	8
Male	3	3	5	11
Body mass				
Small	0	8	0	8
Medium	5	3	5	13
Large	1	1	1	3

Table 2b. Comparison of models for average maximal depth per week during the pre-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random effects	df	AIC	Test	*P*
1	Date, Seal ID	10	1343.69		
2	**Seal ID**	**8**	**1362.87**	**1 vs. 2**	**<0.001**
3	Site, Seal ID	13	1369.81	2 vs. 3	0.692
4	Site	8	1437.84		
5	Date, Site	8	1453.95		
6	Date	8	1466.11		
7	Seal ID, Date, Site	8	1472.36		

Table 2c. Comparison of models for average maximal depth per week during the pre-pupping season. The models include all fixed effects and seal ID, which was the significant random effect.

Model #	Fixed effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**1387.86**		
2	Sex, body mass	6	1390.67	1 vs 2	0.554
3	Sex * body mass	8	1391.64		
4	Sex	5	1394.59		

Table 2d. Results of the most parsimonious linear mixed effect model for average maximal depth per week during the pre-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	*F*	*P*
(Intercept)	1	72.92	<0.001
Body mass	**1**	**7.99**	**0.010**

Tables 3a–d. Post-pupping average maximal depth sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 3a. Sample size from each capture location by sex and by body mass for post-pupping average maximal depth per week.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	0	4	2	6
Pregnant	2	5	5	12
Male	1	3	10	14
Body mass				
Small	0	8	6	14
Medium	3	3	7	13
Large	0	1	4	5

Table 3b. Comparison of models for average maximal depth per week during the post-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	1294.60		
2	**Seal ID**	**8**	**1315.44**	**1 vs 2**	**<0.001**
3	Site and Seal ID	13	1322.63	2 vs 3	0.729
4	Date and Site	10	1414.57		
5	Site	8	1434.96		
6	Seal ID, Date, and Site	8	1514.97		
7	Date	8	1514.97		

Table 3c. Comparison of models for average maximal depth per week during the post-pupping season. The model includes all fixed effects and seal ID, the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**1341.70**		
2	Sex	5	1344.10	1 vs 2	0.532
3	Sex + Body mass	6	1344.40		
4	Sex * Body mass	8	1346.23		

Table 3d. Results of the most parsimonious linear mixed effect model for average maximal depth per week during the post-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	73.91	<0.001
Body mass	1	3.11	0.087

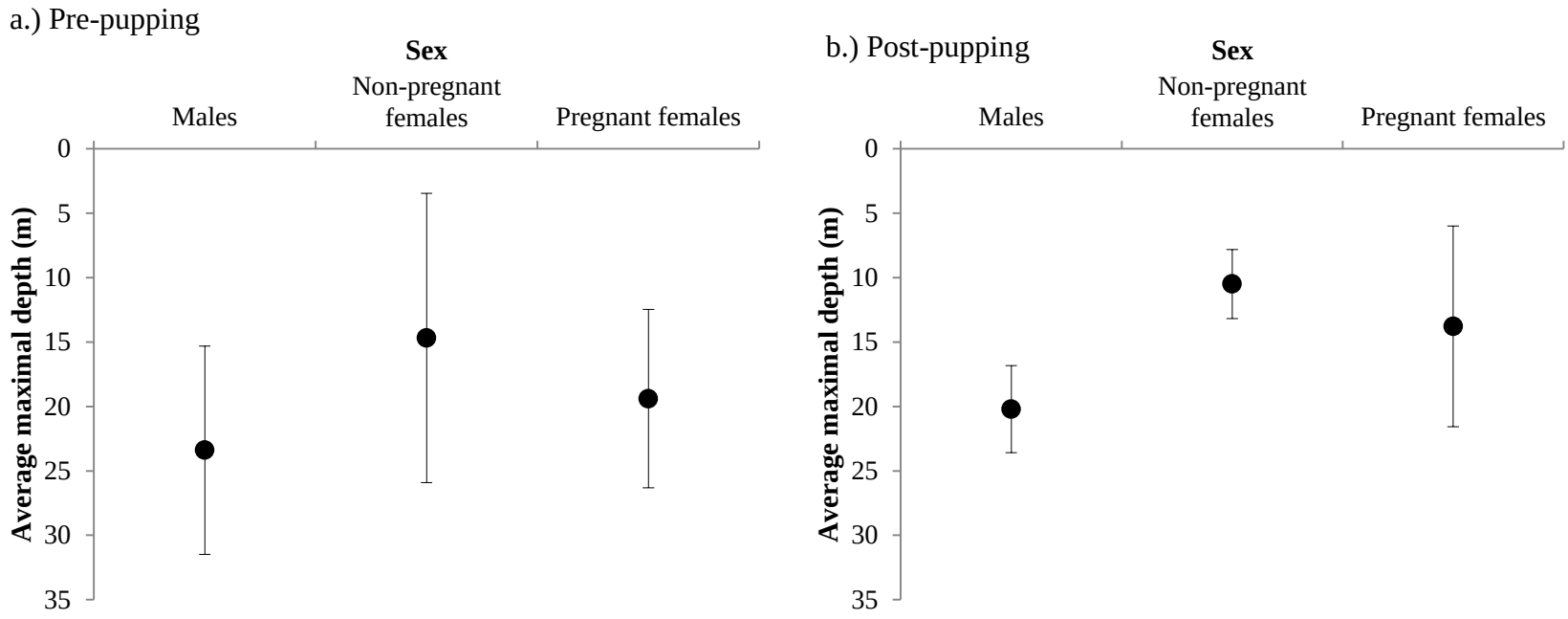


Figure 3. Average maximal depth (m) by sex. a.) Pre-pupping season, b.) Post-pupping season. No significance differences were found. Error bars show standard deviation.

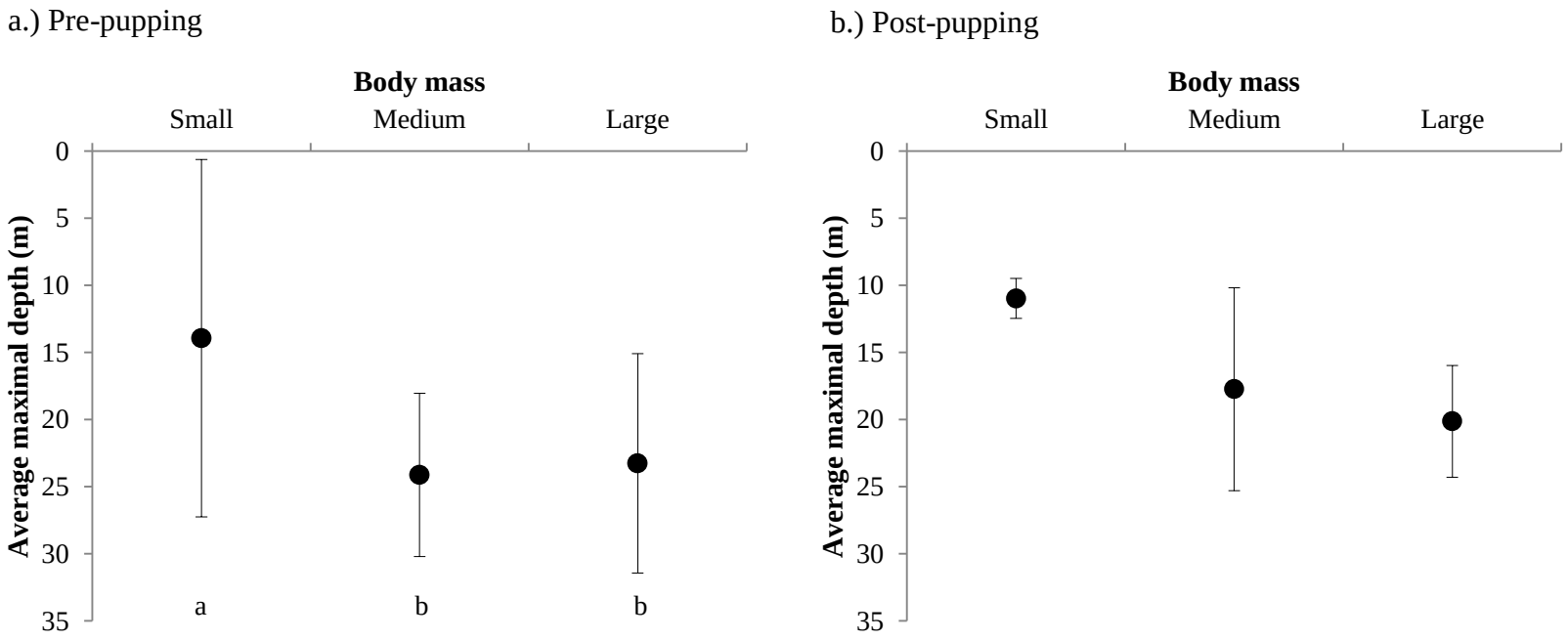


Figure 4. Average maximal depth (m) by body mass. a.) Pre-pupping season (small significantly shallower than medium and large, as indicated by a, b, and b, respectively; pairwise t-test with Bonferroni correction; $P < 0.001$, $p = 0.002$, respectively), b.) Post-pupping season (no significant differences found). Error bars show standard deviation.

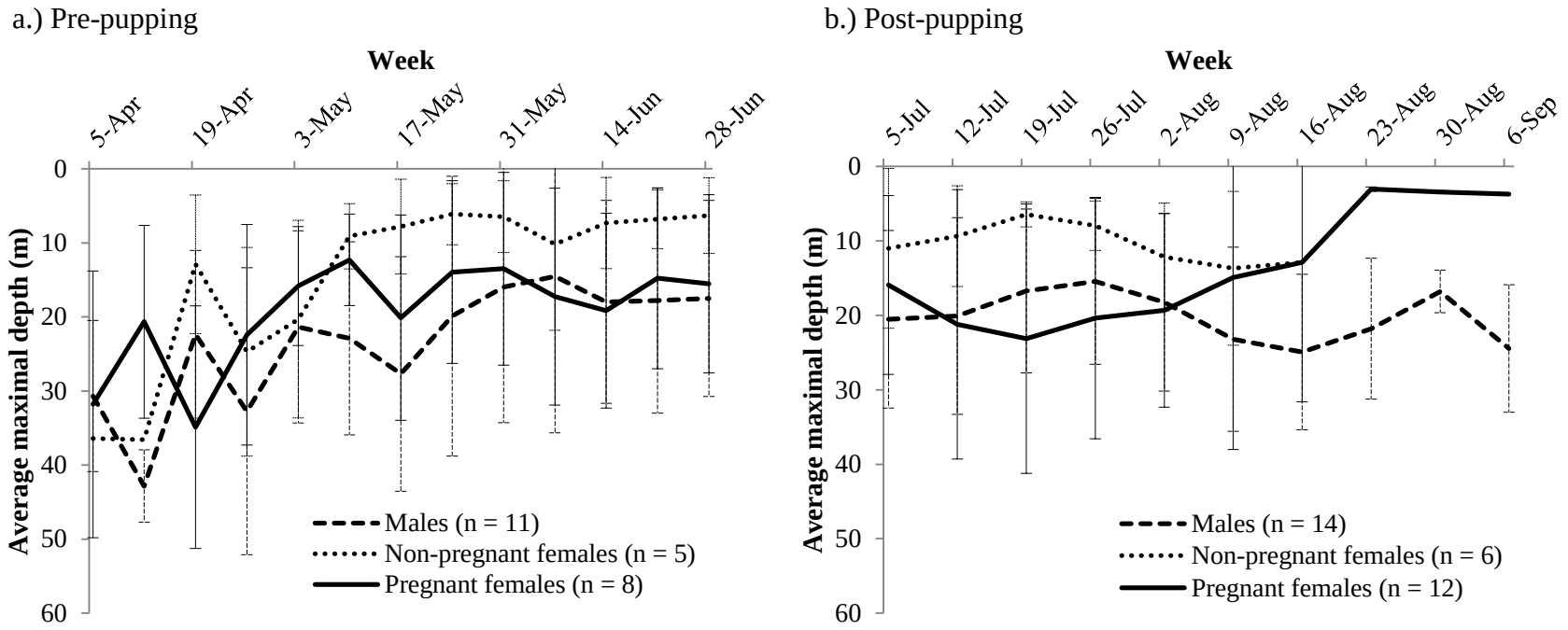


Figure 5. Weekly averages of maximal depth (m) by sex. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each sex category.

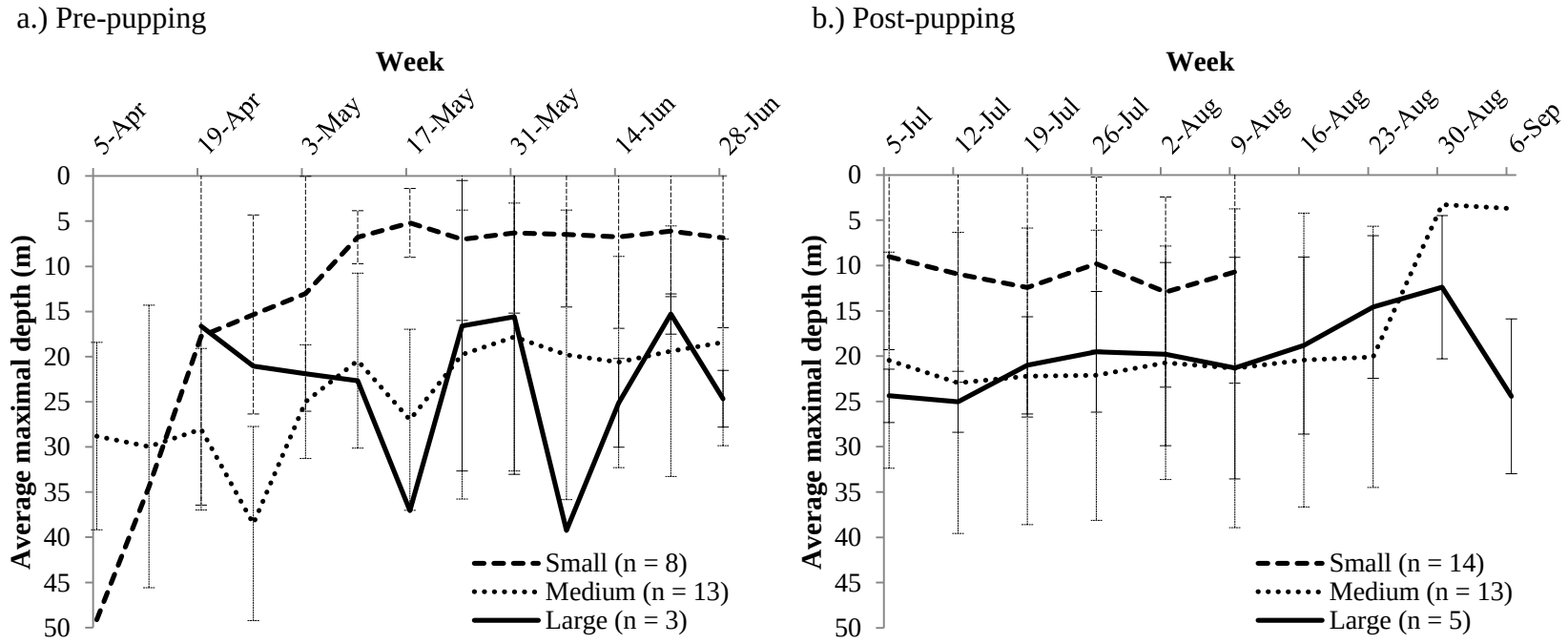


Figure 6. Weekly averages of maximal depth (m) by body mass. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each body mass category.

Average Weekly Dive Duration

Average weekly dive duration was not influenced by sex during either the pre- or post-pupping season (Tables 4a–c and 5a–c; Figures 7–10), nor was it influenced by body mass during the pre-pupping season (Tables 5a–c; Figure 8a). Duration was influenced by body mass during the post-pupping season, supporting that they maintain their mass by spending more time foraging (Tables 5a–d; Figure 8b). One medium-sized male seal from Bird Rocks was removed from the analysis of this variable because his recorded dive durations were erroneous, showing that his duration per week exceeded the number of hours in a week.

The average weekly dive durations for the entire pre-pupping versus post-pupping seasons by sex were 112 ± 33 hours versus 96 ± 38 hours for males, 106 ± 28 hours versus 94 ± 15 hours for non-pregnant females, and 104 ± 37 hours versus 86 ± 34 hours for pregnant females. There were no significant differences between the pre- and post-pupping seasons for any of the sex categories (two-sample unequal variance t-test; $P > 0.05$).

During the post-pupping season, small seals dived for significantly shorter durations than did medium or large seals. There was no difference between medium and large seals. Small seals initially dived for approximately 80 hours per week, then declined to only 40 hours for the last week of their deployment, the week of August 9 (Figure 10b). Medium seals dived for between 100 and 120 hours per week, then declined to 60 for the last two weeks of the post-pupping season. Large seals dived for 150 hours, then declined over four weeks to 120 hours, finishing the post-pupping season diving approximately 90 hours per week. The average weekly dive durations for the entire pre-pupping versus post-pupping

seasons by body mass were 92 ± 35 hours versus 80 ± 25 hours for small seals, 112 ± 30 hours versus 103 ± 36 hours for medium seals, and 135 ± 10 hours versus 118 ± 17 hours for large seals. These seasonal patterns should be interpreted with caution, however, since there were no significant differences between the seasons (two-sample unequal variance t-test; $P > 0.05$).

Tables 4a–d. Pre-pupping average weekly dive duration sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold font.

Table 4a. Sample size from each capture location by sex and by body mass for pre-pupping average weekly dive duration.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	0	5
Pregnant	2	5	1	8
Male	2	3	5	10
Body mass				
Small	0	8	0	8
Medium	4	3	5	12
Large	1	1	1	3

Table 4b. Comparison of models for average weekly dive duration during the pre-pupping season. The models include different random effects and all fixed effects.

Model #	Random Effects	df	AIC	Test	*P*
1	**Site and Seal ID**	**8**	**3623.05**		
2	Seal ID	8	3623.05		
3	Date and Seal ID	10	3627.05	2 vs 3	1.000
4	Site	8	3732.65		
5	Date and Site	10	3734.87		
6	Date	8	3741.82		
7	Seal ID, Date, and Site	8	3743.08		

Table 4c. Comparison of models for average weekly dive duration during the pre-pupping season. The models include all fixed effects and site and seal ID, the significant random effects.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**3720.24**		
2	Sex	5	3722.07	1 vs 2	0.676
3	Sex + Body mass	6	3722.92		
4	Sex * Body mass	8	3726.54		

Table 4d. Results of the most parsimonious linear mixed effect model for average weekly dive duration during the pre-pupping season. The model includes body mass as the fixed effect and site and seal ID as the random effects. No significance was found.

	numDF	F-value	*P*
(Intercept)	1	62.25	<0.001
Body mass	1	1.44	0.244

Table 5a–d. Post-pupping average weekly dive duration sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 5a. Sample size from each capture location by sex and by body mass for post-pupping average weekly dive duration.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	0	4	2	6
Pregnant	2	5	5	12
Male	1	3	10	14
Body mass				
Small	0	8	6	14
Medium	3	3	7	13
Large	0	1	4	5

Table 5b. Comparison of models for average weekly dive duration during the post-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	3295.62		
2	**Seal ID**	**8**	**3326.21**	**1 vs 2**	**<0.001**
3	Site and Seal ID	13	3335.23	2 vs 3	0.965
4	Site	8	3384.08		
5	Date and Site	8	3396.80		
6	Seal ID, Date, and Site	8	3400.04		
7	Date	8	3400.04		

Table 5c. Comparison of models for average weekly dive duration during the post-pupping season. The models include all fixed effects and seal ID, which was the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**3414.84**		
2	Sex * Body mass	8	3415.25	1 vs 2	0.108
3	Sex + Body mass	6	3417.38		
4	Sex	5	3422.30		

Table 5d. Results of the most parsimonious linear mixed effect model for average weekly dive duration during the post-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	388.19	<0.001
Body mass	**1**	**8.17**	**0.007**

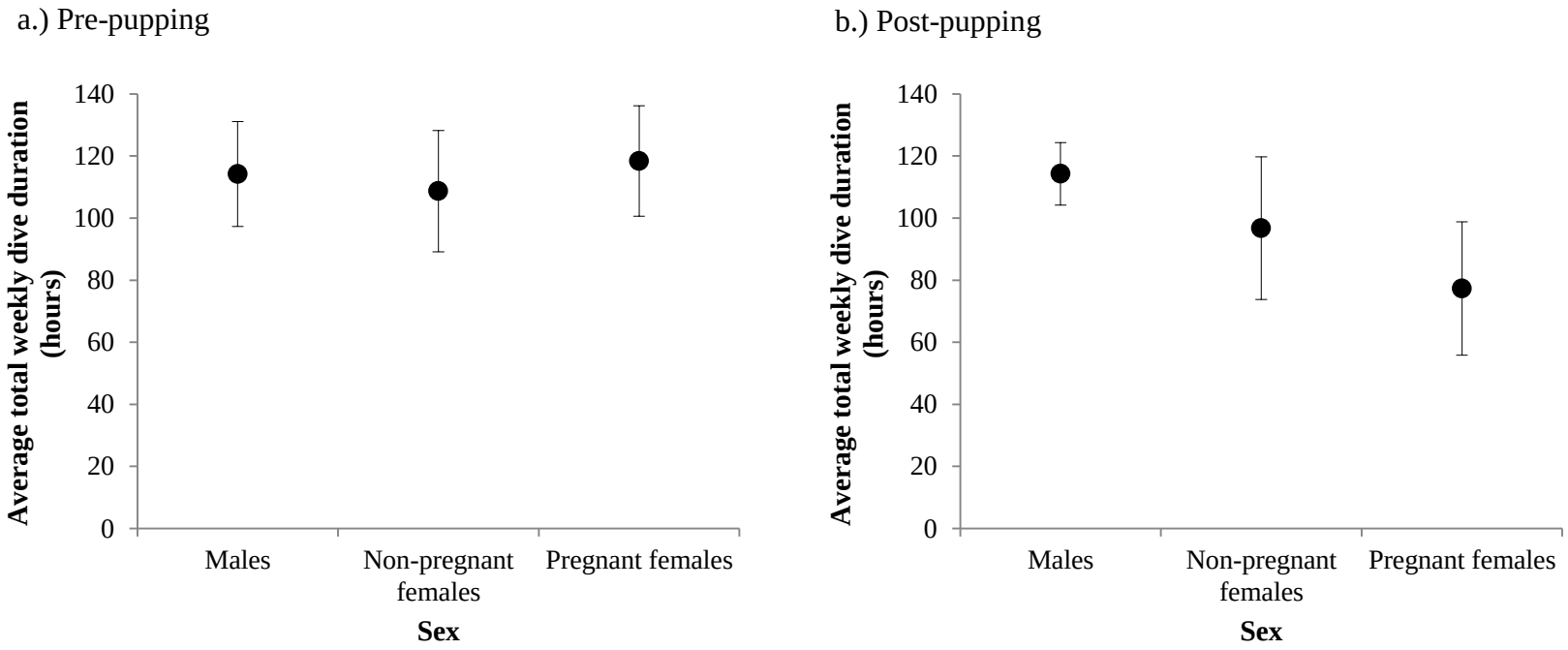


Figure 7. Average total weekly dive duration (hours) by sex. a.) Pre-pupping season, b.) Post-pupping season. No significant differences were found. Error bars show standard deviation.

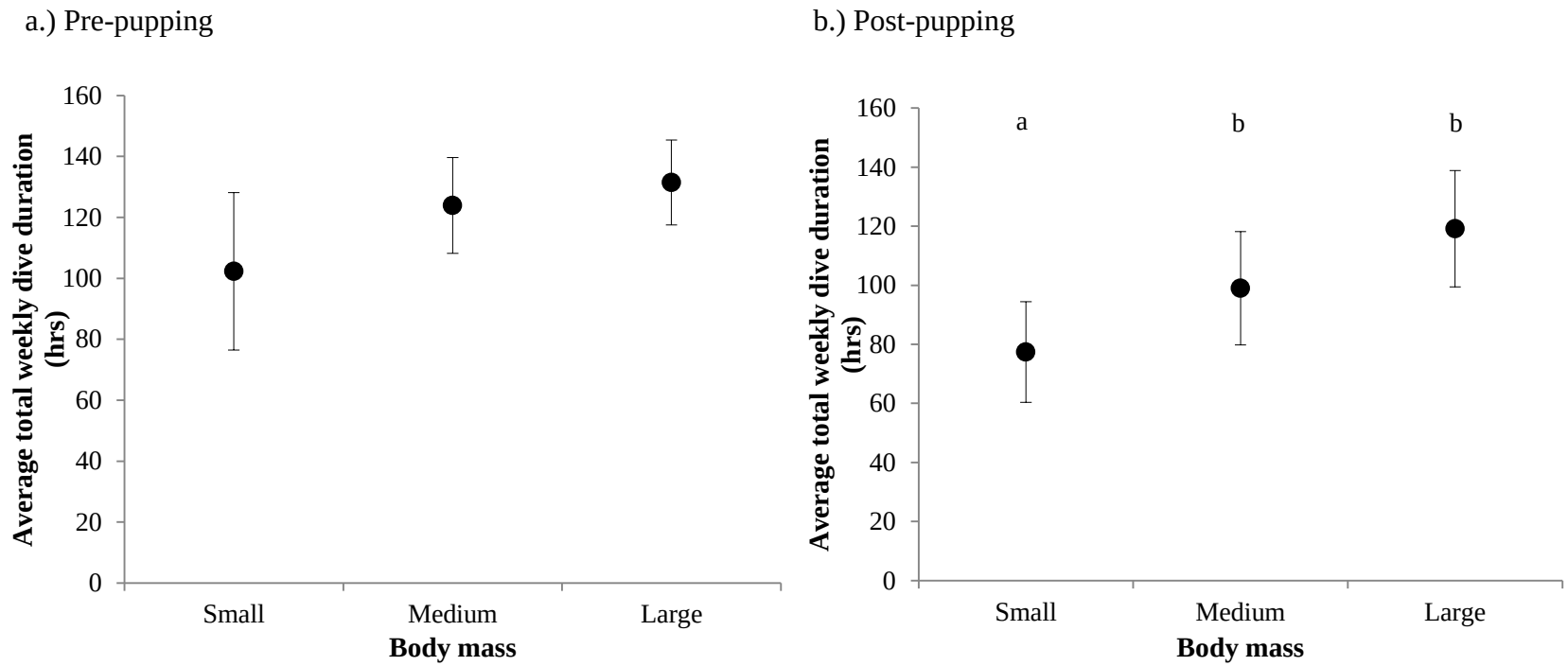


Figure 8. Average total weekly dive duration (hours) by body mass. a.) Pre-pupping season, b.) Post-pupping season (small significantly shorter than medium and large, as indicated by a, b, and b, respectively; pairwise t-test with Bonferroni correction; $P < 0.001$ for both comparisons, no difference between medium and large seals). Error bars show standard deviation.

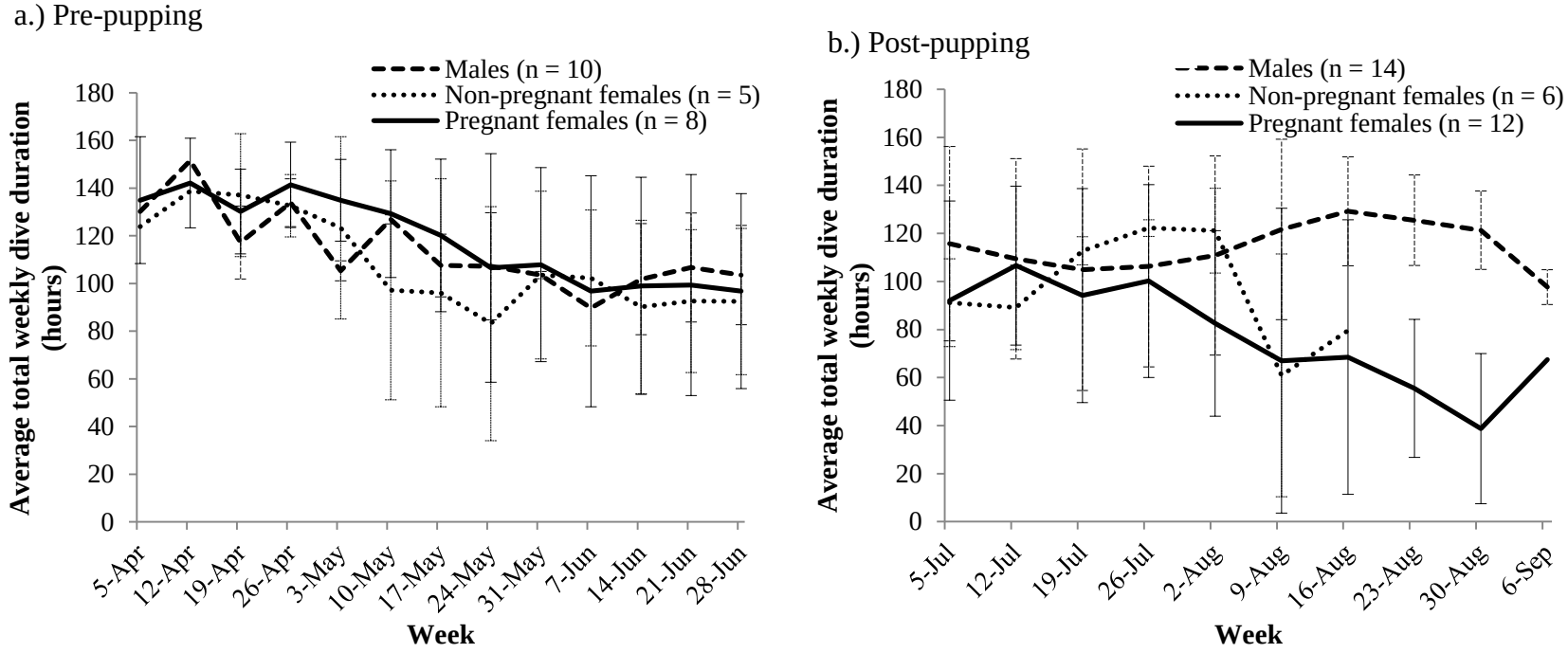


Figure 9. Per week average weekly dive duration (hours) by sex. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each sex category.

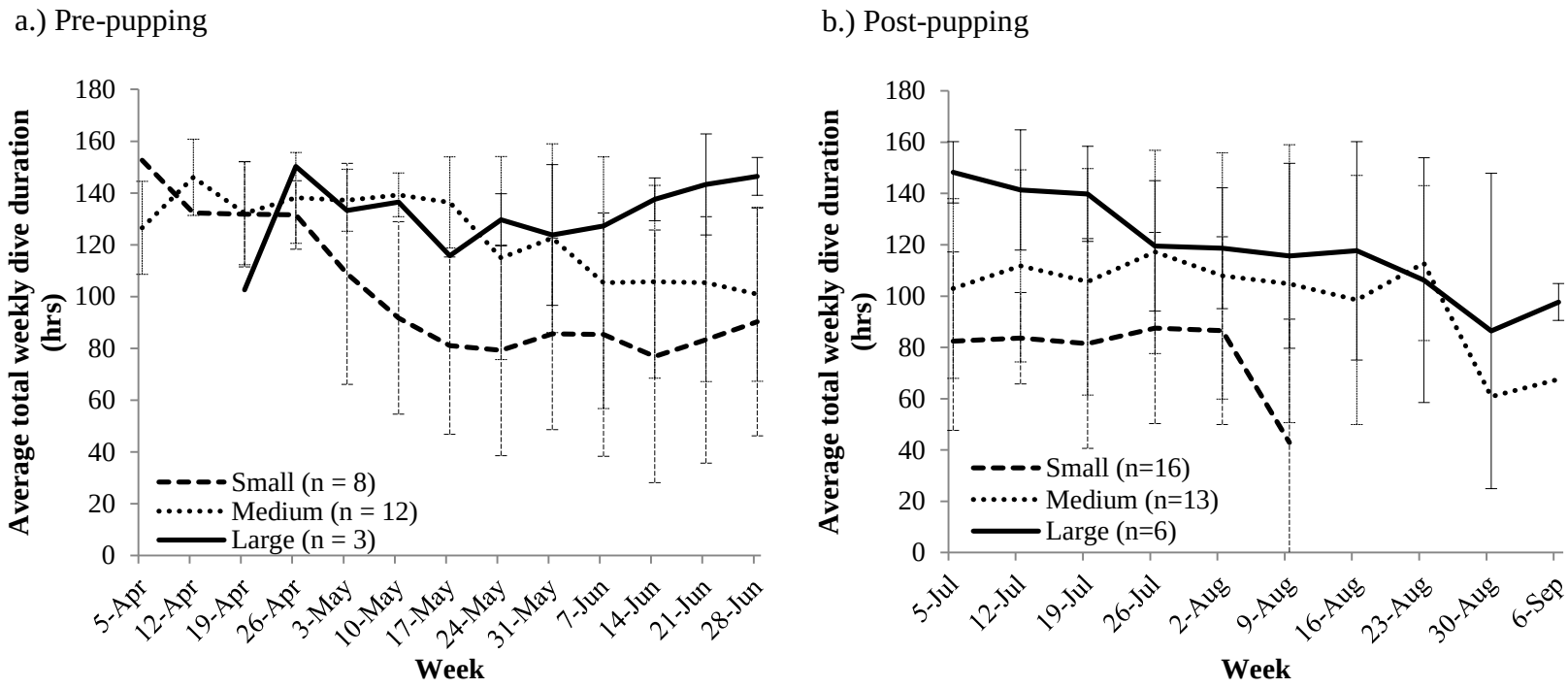


Figure 10. Per week average weekly dive duration (hours) by body mass. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each body mass category.

Average Number of Dives per Week

Average number of dives per week was not influenced by sex or body mass during either the pre- or post-pupping seasons (Tables 6 and 7; Figures 11–14). The average number of dives per week for the pre-pupping versus post-pupping seasons by sex were 1,592 ± 772 dives versus 1,317 ± 619 dives for males, 1,477 ± 322 dives versus 1,483 ± 494 dives for non-pregnant females, and 1,281 ± 400 dives versus 1,350 ± 502 dives for pregnant females. There were no significant differences by sex between the seasons (two-sample unequal variance t-test; $P > 0.05$).

The average number of dives per week for the entire pre-pupping versus post-pupping seasons by body mass were 1623 ± 832 dives versus 1,247 ± 583 dives for small seals, 1,356 ± 462 dives versus 1,480 ± 475 dives for medium seals, and 1,508 ± 293 dives versus 1,616 ± 309 dives for large seals. There were no significant differences between the seasons (two-sample unequal variance t-test; $P > 0.05$).

Tables 6a–d. Pre-pupping average number of dives per week sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 6a. Sample size from each capture location by sex and by body mass for pre-pupping average number of dives per week.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	0	5
Pregnant	2	5	1	8
Male	3	3	5	11
Body mass				
Small	0	8	0	8
Medium	5	3	5	13
Large	1	1	1	3

Table 6b. Comparison of models for average number of dives per week during the pre-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	2879.23		
2	**Seal ID**	**8**	**2886.56**	**1 vs 2**	**0.004**
3	Site and Seal ID	13	2890.22	2 vs 3	0.275
4	Seal ID, Date, and Site	8	2960.66		
5	Date and Site	8	2960.66		
6	Date	8	2960.66		
7	Site	8	2960.66		

Table 6c. Comparison of models for average number of dives per week during the pre-pupping season. The models include all fixed effects and seal ID, which was the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**2959.31**		
2	Sex	5	2960.28	1 vs 2	0.310
3	Sex + Body mass	6	2961.77		
4	Sex * Body mass	8	2964.74		

Table 6d. Results of the most parsimonious linear mixed effect model for average dives per week during the pre-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	161.53	<0.001
Body mass	1	0.42	0.522

Tables 7a–d. Post-pupping average number of dives per week sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 7a. Sample size from each capture location by sex and by body mass for post-pupping average number of dives per week.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	0	4	2	6
Pregnant	2	5	5	12
Male	1	3	10	14
Body mass				
Small	0	8	6	14
Medium	3	3	7	13
Large	0	1	4	5

Table 7b. Comparison of models for average number of dives per week during the post-pupping season. The models include different random effects and all fixed effects.

Model #	Random Effects	df	AIC	Test	*P*
1	**Seal ID**	**8**	**2895.46**		
2	Date and Seal ID	10	2896.26	1 vs 2	0.202
3	Site and Seal ID	13	2905.43		
4	Date and Site	10	2944.43		
5	Site	8	2944.96		
6	Date	8	2946.08		
7	Seal ID, Date, and Site	8	2946.14		

Table 7c. Comparison of models for average number of dives per week during the post-pupping season. The models include all fixed effects and seal ID, which was the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**2967.36**		
2	Sex * Body mass	8	2969.38	1 vs 2	0.201
3	Sex + Body mass	6	2970.40		
4	Sex	5	2971.57		

Table 7d. Results of the most parsimonious linear mixed effect model for average number of dives per week during the post-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	302.01	<0.001
Body mass	1	2.64	0.114

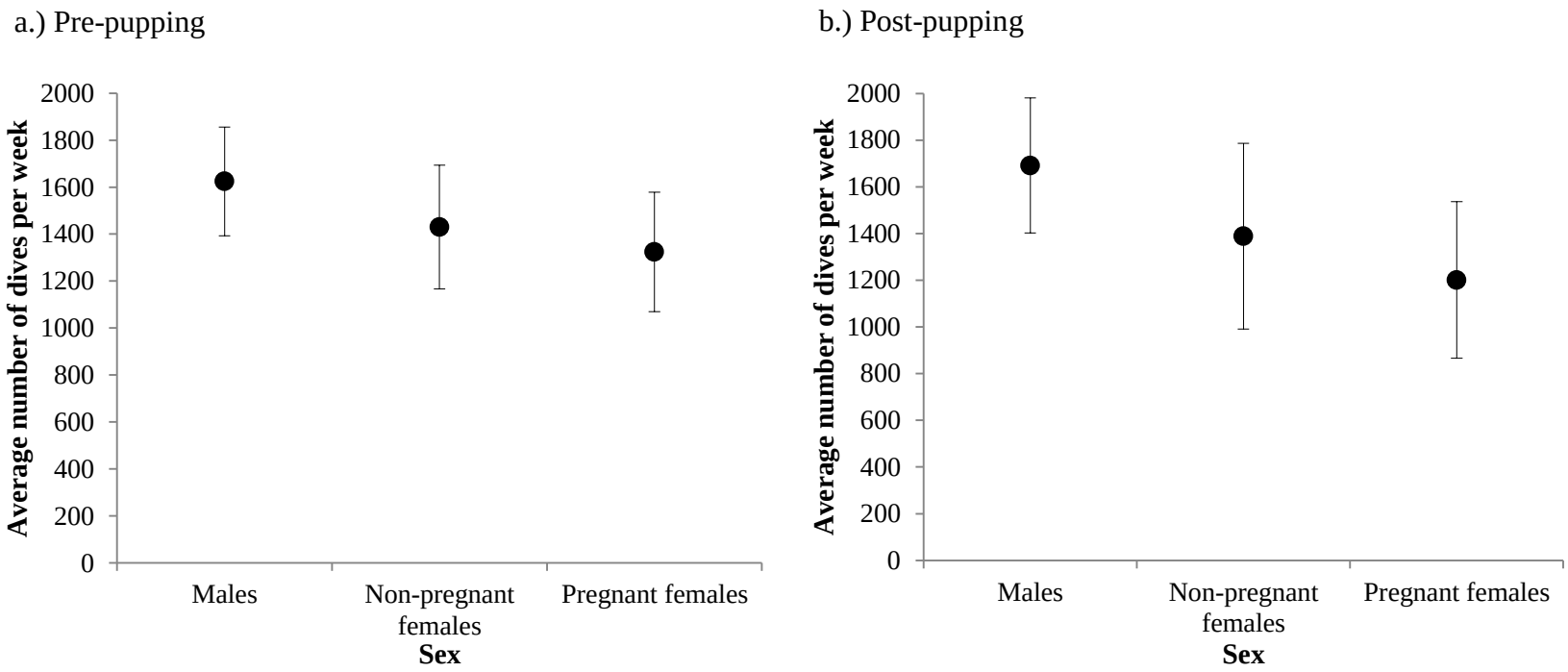


Figure 11. Average number of dives per week by sex. a.) Pre-pupping season, b.) Post-pupping season. No significant differences were found. Error bars show standard deviation.

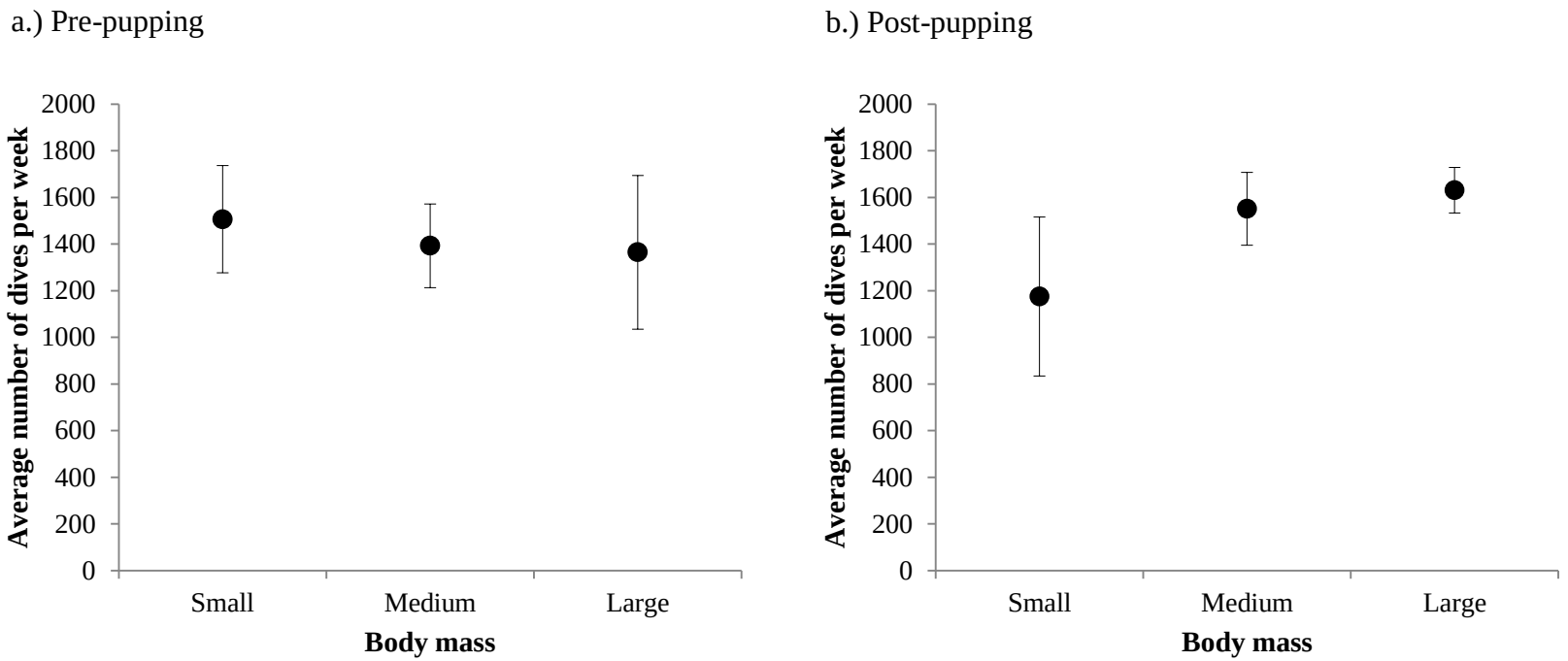


Figure 12. Average number of dives per week by body mass. a.) Pre-pupping season, b.) Post-pupping season. No significance was found. Error bars show standard deviation.

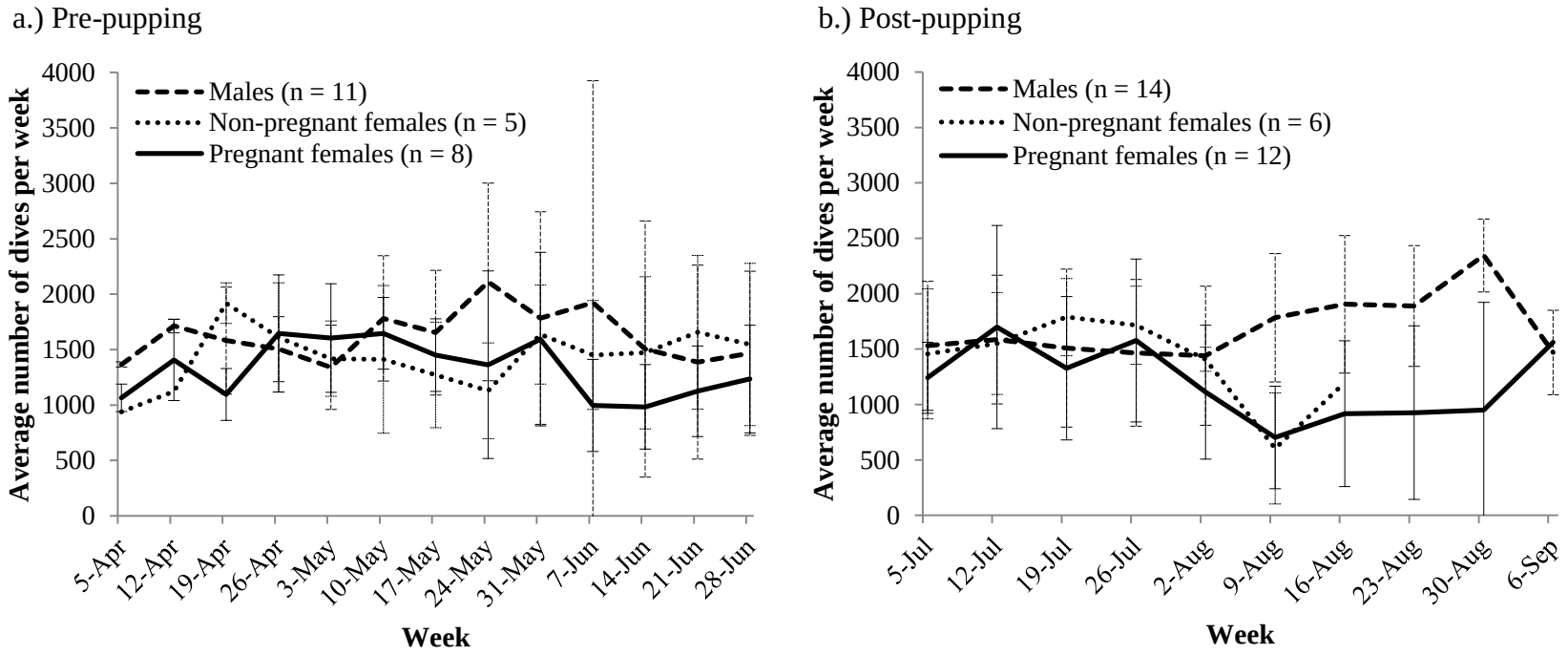


Figure 13. Weekly average number of dives by sex. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each sex category.

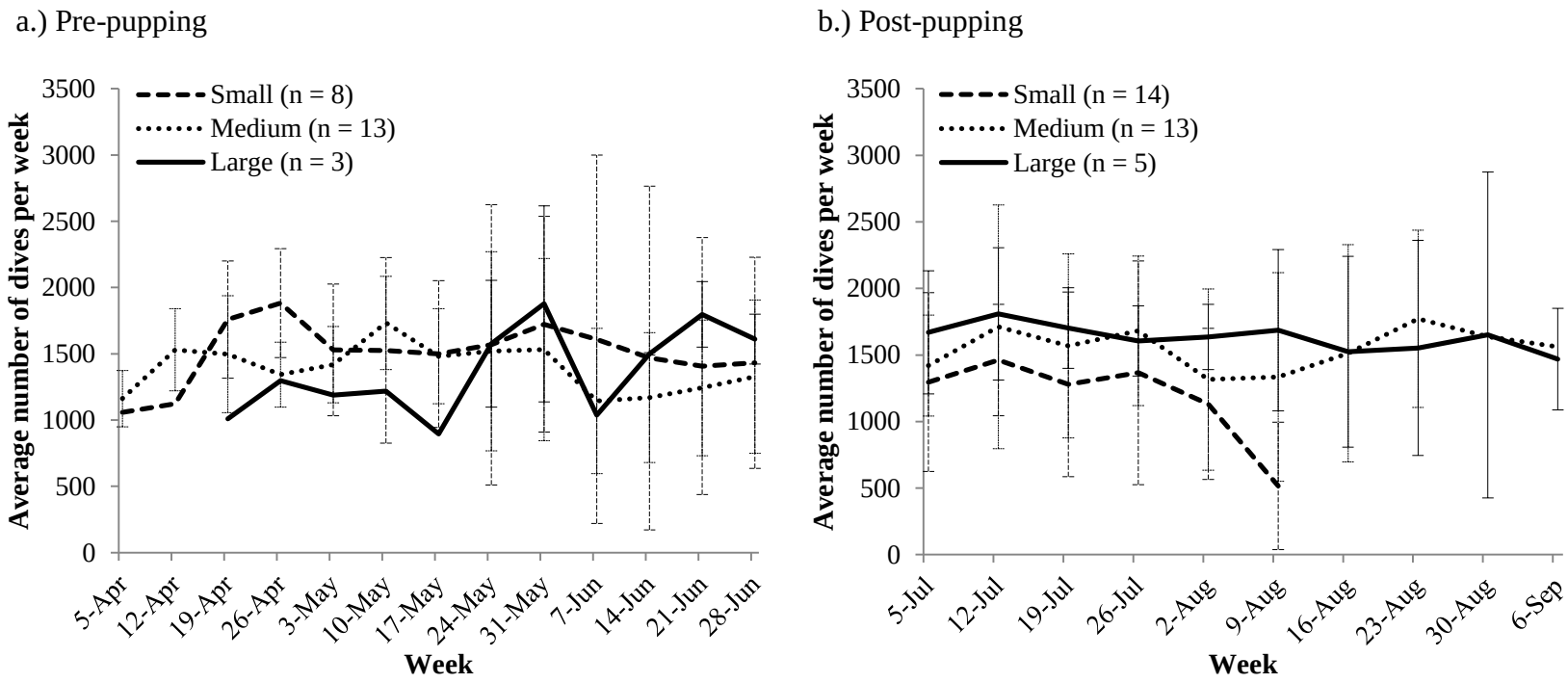


Figure 14. Weekly average number of dives by body mass. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each body mass category.

Average Number of Diving Bouts/Week

Average number of bouts per week was not influenced by sex or body mass during either the pre- or post-pupping seasons (Tables 8 and 9; Figures 15–18). The average number of bouts per week for the entire pre-pupping versus post-pupping seasons by sex were 107 ± 74 hours versus 91 ± 47 hours for males, 100 ± 25 hours versus 108 ± 55 hours for non-pregnant females, and 86 ± 49 hours versus 122 ± 83 hours for pregnant females. There were no significant differences between the seasons by sex (two-sample unequal variance t-test; $P > 0.05$).

The average number of bouts per week for the entire pre-pupping versus post-pupping seasons by body mass were 126 ± 64 bouts versus 108 ± 69 bouts for small seals, 88 ± 54 bouts versus 107 ± 63 bouts for medium seals, and 71 ± 35 bouts versus 105 ± 37 bouts for large seals. There were no significant differences between the seasons (two-sample unequal variance t-test; $P > 0.05$).

Tables 8a–d. Pre-pupping average number of bouts per week sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 8a. Sample size from each capture location by sex and by body mass for pre-pupping average number of bouts per week.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	0	5
Pregnant	2	5	1	8
Male	3	3	5	11
Body mass				
Small	0	8	0	8
Medium	5	3	5	13
Large	1	1	1	3

Table 8b. Comparison of models for average number of bouts per week during the pre-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	2003.97		
2	**Seal ID**	**8**	**2007.16**	**1 vs 2**	**0.027**
3	Site and Seal ID	13	2013.48	2 vs 3	0.596
4	Site	8	2061.31		
5	Date and Site	8	2063.73		
6	Date	8	2066.32		
7	Seal ID, Date, and Site	8	2069.50		

Table 8c. Comparison of models for average number of bouts per week during the pre-pupping season. The models include all fixed effects and seal ID, the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**2053.43**		
2	Sex * Body mass	8	2055.92	1 vs 2	0.239
3	Sex + Body mass	6	2056.16		
4	Sex	5	2057.81		

Table 8d. Results of the most parsimonious linear mixed effect model for average bouts per week during the pre-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	85.54	<0.001
Body mass	1	3.37	0.080

Tables 9a–d. Post-pupping average number of bouts per week sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 9a. Sample size from each capture location by sex and by body mass for post-pupping average number of bouts per week.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	0	4	2	6
Pregnant	2	5	5	12
Male	1	3	10	14
Body mass				
Small	0	8	6	14
Medium	3	3	7	13
Large	0	1	4	5

Table 9b. Comparison of models for average number of bouts per week during the post-pupping season. The models include different random effects and all fixed effects.

Model #	Random Effects	df	AIC	Test	*P*
1	**Seal ID**	**8**	**2093.32**		
2	Date and Seal ID	10	2097.32	1 vs 2	1.000
3	Site and Seal ID	13	2102.43		
4	Seal ID, Date, and Site	8	2159.72		
5	Date	8	2159.72		
6	Site	8	2159.72		
7	Date and Site	10	2162.25		

Table 9c. Comparison of models for average number of bouts per week during the post-pupping season. The models include all fixed effects and seal ID, the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**2136.64**		
2	Sex	5	2137.38	1 vs 2	0.262
3	Sex + Body mass	6	2139.38		
4	Sex * Body mass	8	2142.85		

Table 9d. Results of the most parsimonious linear mixed effect model for average number of bouts per week during the post-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	113.29	<0.001
Body mass	1	0.05	0.823

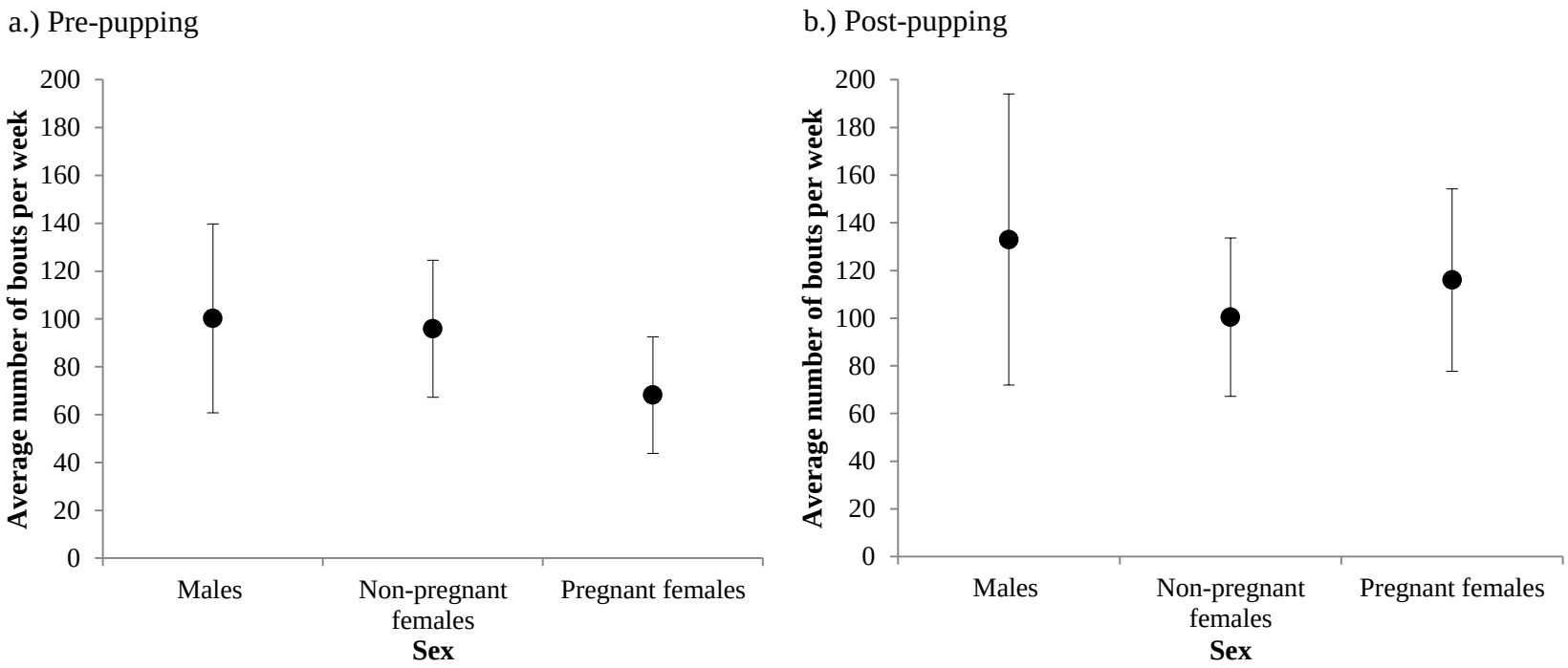


Figure 15. Average number of bouts per week by sex. a.) Pre-pupping season, b.) Post-pupping season. No significant differences were found. Error bars show standard deviation.

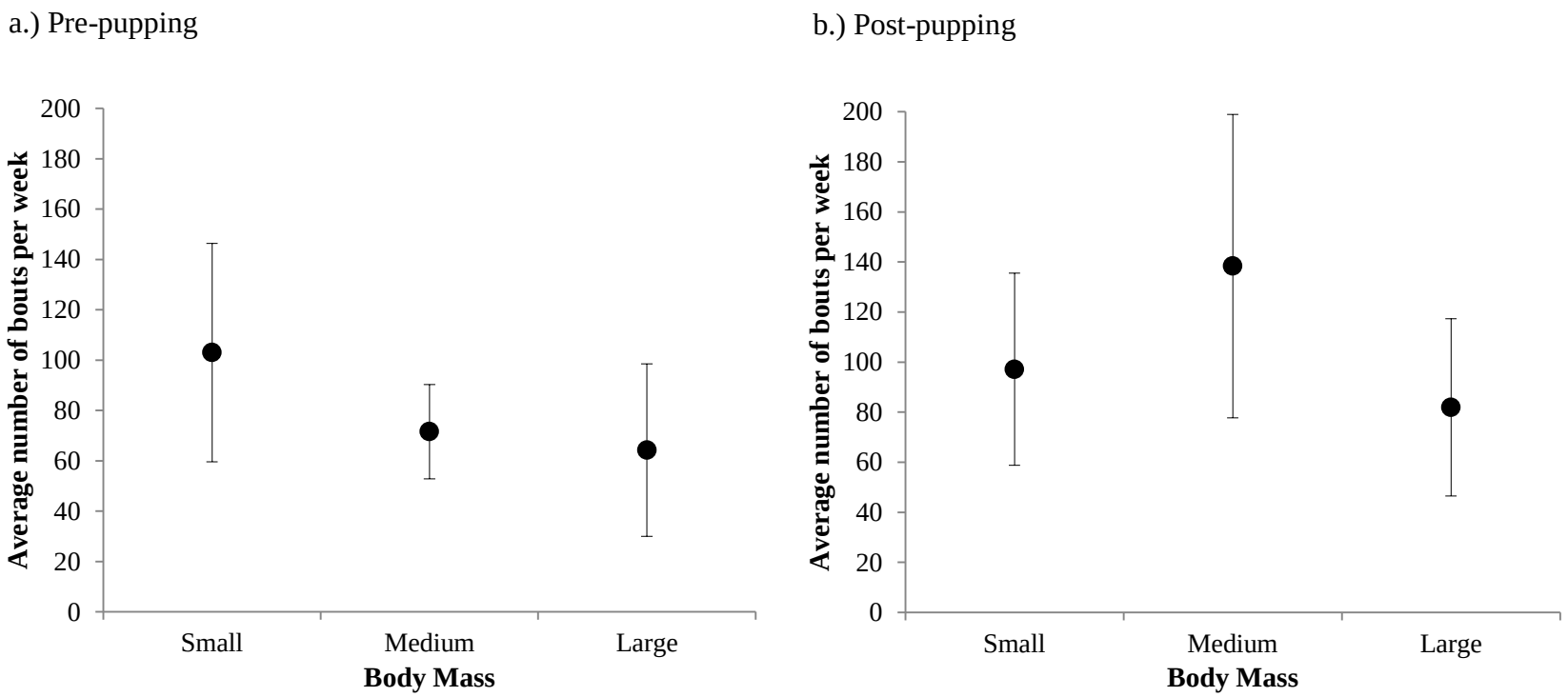
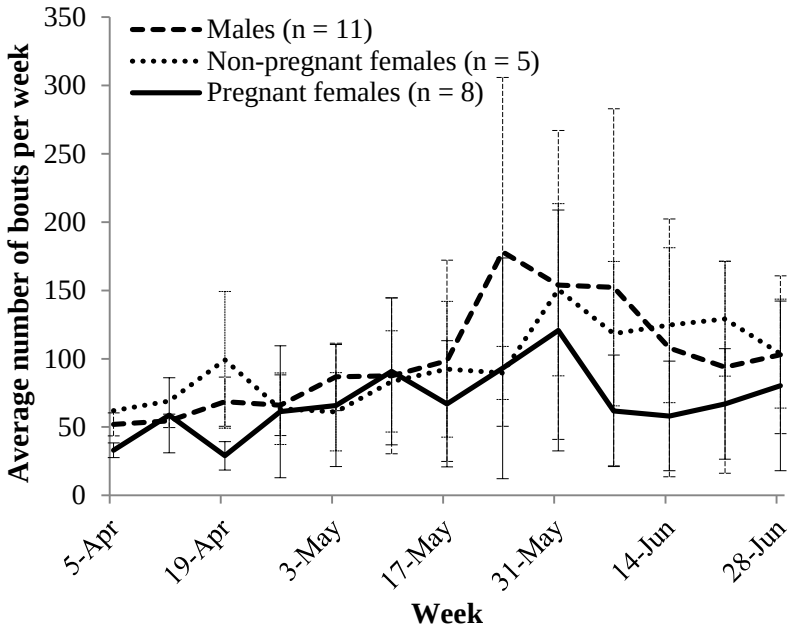


Figure 16. Average number of bouts per week by body mass. a.) Pre-pupping season, b.) Post-pupping season. No significant differences were found. Error bars show standard deviation.

a.) Pre-pupping



b.) Post-pupping

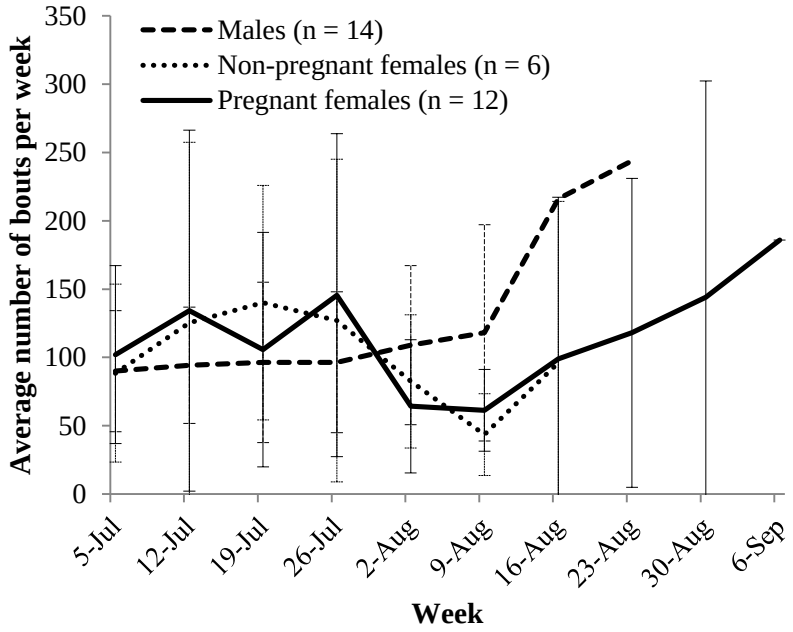
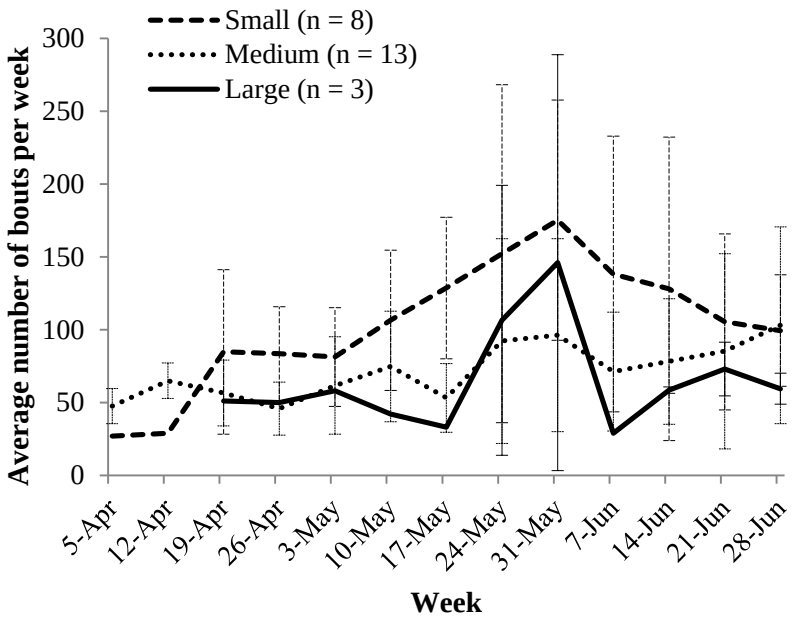


Figure 17. Weekly average number of bouts by sex. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each sex category.

a.) Pre-pupping



b.) Post-pupping

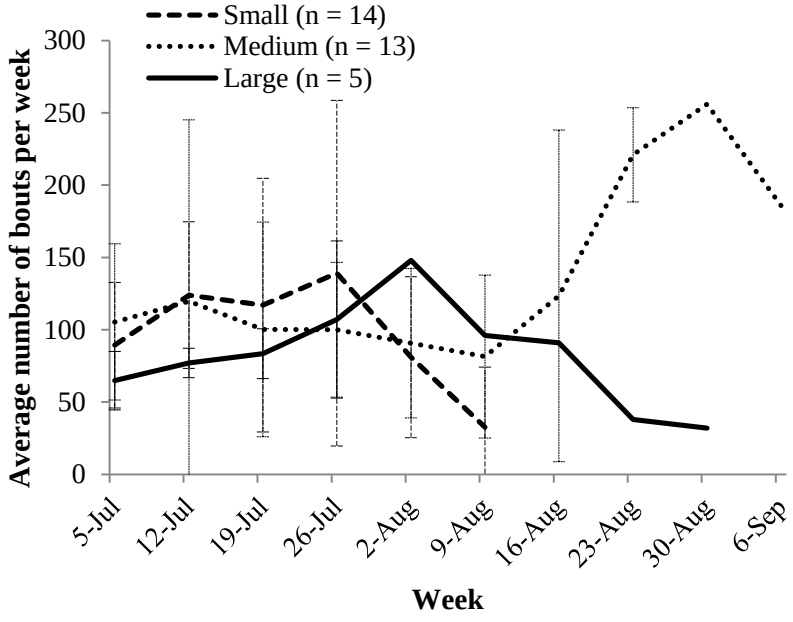


Figure 18. Per week average number of bouts by body mass. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each body mass category.

Dive-profile Index

Body mass significantly influenced DPI during both the pre- and post-pupping seasons (Tables 10 and 11, Figure 20). Sex did not influence DPI during either season (Tables 10a–c and 11a–c; Figures 19 and 21).

Average DPI by sex for the entire pre- versus post-pupping seasons were 51,054 ± 16,083 versus 49,817 ± 7,856 for males, 30,680 ± 18,082 versus 28,689 ± 6,781 for non-pregnant females, and 43,659 ± 14,200 versus 31,004 ± 20,178 for pregnant females. None of these were significantly different by season (two-sample unequal variance t-test; $P > 0.05$).

Body mass had a significant influence on DPI during both the pre- and post-pupping seasons (Tables 10 and 11; Figures 20a and b). During both seasons, small seals had a lower average DPI than medium or large seals. No differences were found between medium and large seals in either season.

During the pre-pupping season, initial average DPI for small seals was greater than 100,000 dropping to 20,000 by May 17 where it stayed for the remainder of the season (Figure 22a). Average DPI of medium seals was approximately 65,000 at the beginning of the pre-pupping season, gradually decreasing to 40,000 before increasing back to 50,000 for the duration of the season. Average DPI of large seals was approximately 40,000 throughout the pre-pupping season with peaks to 70,000.

Small seals began the post-pupping season with an average DPI of 20,000, steadily increasing to 32,000 where it stayed until the end of the deployment. Average DPI of

medium and large seals remained between 50,000 and 60,000, with DPI of medium seals decreasing to 7,000 for the last two weeks of the deployment (Figure 22b).

Average DPI by body mass for the entire pre- versus post-pupping seasons were 18,743 ± 20,818 versus 31,814 ± 28,065 for small seals, 50,275 ± 24,821 versus 57,516 ± 27,230 for medium seals, and 50,688 ± 4,071 versus 50,232 ± 16,409 for large seals. None of these were significantly different (two-sample unequal variance t-test; $P > 0.05$).

Table 10a–d. Pre-pupping average weekly dive profile index sample sizes and linear mixed-effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 10a. Sample size from each capture location by sex and by body mass for pre-pupping average weekly dive profile index.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	1	4	0	5
Pregnant	2	5	1	8
Male	3	3	5	11
Body mass				
Small	0	8	0	8
Medium	5	3	5	13
Large	1	1	1	3

Table 10b. Comparison of models for average weekly dive profile index during the pre-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	4102.30		
2	**Seal ID**	**8**	**4135.24**	**1 vs 2**	**<0.001**
3	Site and Seal ID	13	4144.90	2 vs 3	0.997
4	Site	8	4261.13		
5	Date and Site	8	4269.78		
6	Date	8	4272.10		
7	Seal ID, Date, and Site	8	4277.79		

Table 10c. Comparison of models for average weekly dive profile index during the pre-pupping season. The models include all fixed effects and seal ID, the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**4253.05**		
2	Sex + Body mass	6	4255.21	1 vs 2	0.398
3	Sex * Body mass	8	4257.20	2 vs 3	0.365
4	Sex	5	4259.15	3 vs 4	0.047

Table 10d. Results of the most parsimonious linear mixed effect model for average weekly dive profile index during the pre-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	75.87	<0.001
Body mass	**1**	**8.25**	**0.009**

Table 11a–d. Post-pupping average weekly dive profile index sample sizes and linear mixed effects model summary. Statistically significant results ($P < 0.05$) or the best model are indicated by bold text.

Table 11a. Sample size from each capture location by sex and by body mass for post-pupping average weekly dive profile index.

Attribute	Location			Total
	Bird Rocks	Padilla Bay	Hood Canal	
Sex/status				
Female				
Non-pregnant	0	4	2	6
Pregnant	1	3	9	11
Male	1	3	9	13
Body mass				
Small	0	8	6	14
Medium	2	3	6	11
Large	0	1	4	5

Table 11b. Comparison of models for average weekly dive profile index during the post-pupping season. The models include different random effects and all fixed effects. In this case, Model 2 was the most parsimonious model when compared to Model 1 via ANOVA (shown in bold).

Model #	Random Effects	df	AIC	Test	*P*
1	Date and Seal ID	10	3913.02		
2	**Seal ID**	**8**	**3935.27**	**1 vs 2**	**<0.001**
3	Site and Seal ID	13	3942.96	2 vs 3	0.806
4	Date and Site	10	4021.82	3 vs 4	<0.001
5	Site	8	4024.91	4 vs 5	0.029
6	Seal ID, Date, and Site	8	4124.45		
7	Date	8	4124.45		

Table 11c. Comparison of models for average weekly dive profile index during the post-pupping season. The models include all fixed effects and seal ID, which was the significant random effect.

Model #	Fixed Effects	df	AIC	Test	*P*
1	**Body mass**	**4**	**4054.23**		
2	Sex + Body mass	6	4056.47	1 vs 2	0.415
3	Sex	5	4057.51	2 vs 3	0.081
4	Sex * Body mass	8	4057.65	3 vs 4	0.119

Table 11d. Results of the most parsimonious linear mixed effect model for average weekly dive profile index during the post-pupping season. The model includes body mass as the fixed effect and seal ID as the random effect.

	numDF	F-value	*P*
(Intercept)	1	97.89	<0.001
Body mass	**1**	**4.28**	**0.047**

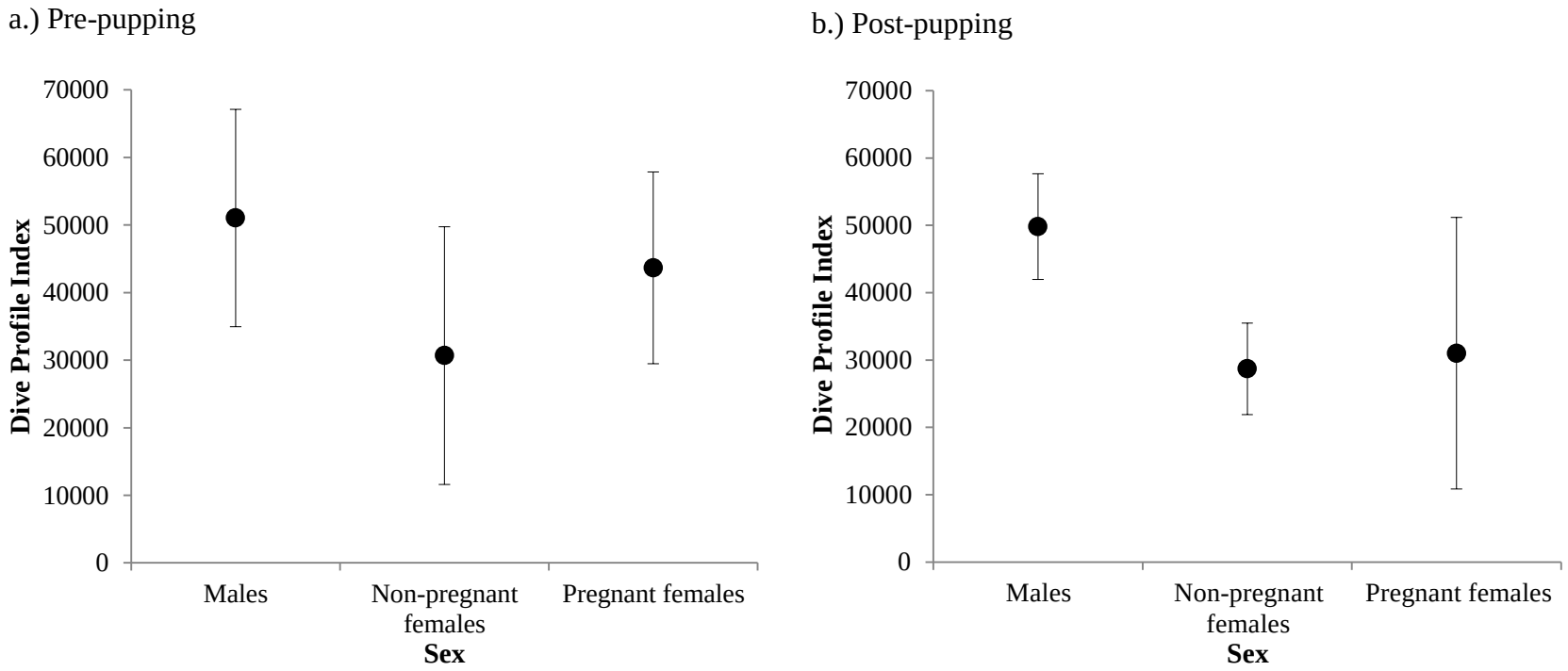


Figure 19. Average total weekly dive profile index by sex. a.) Pre-pupping season, b.) Post-pupping season. No significant differences were found. Error bars show standard deviation.

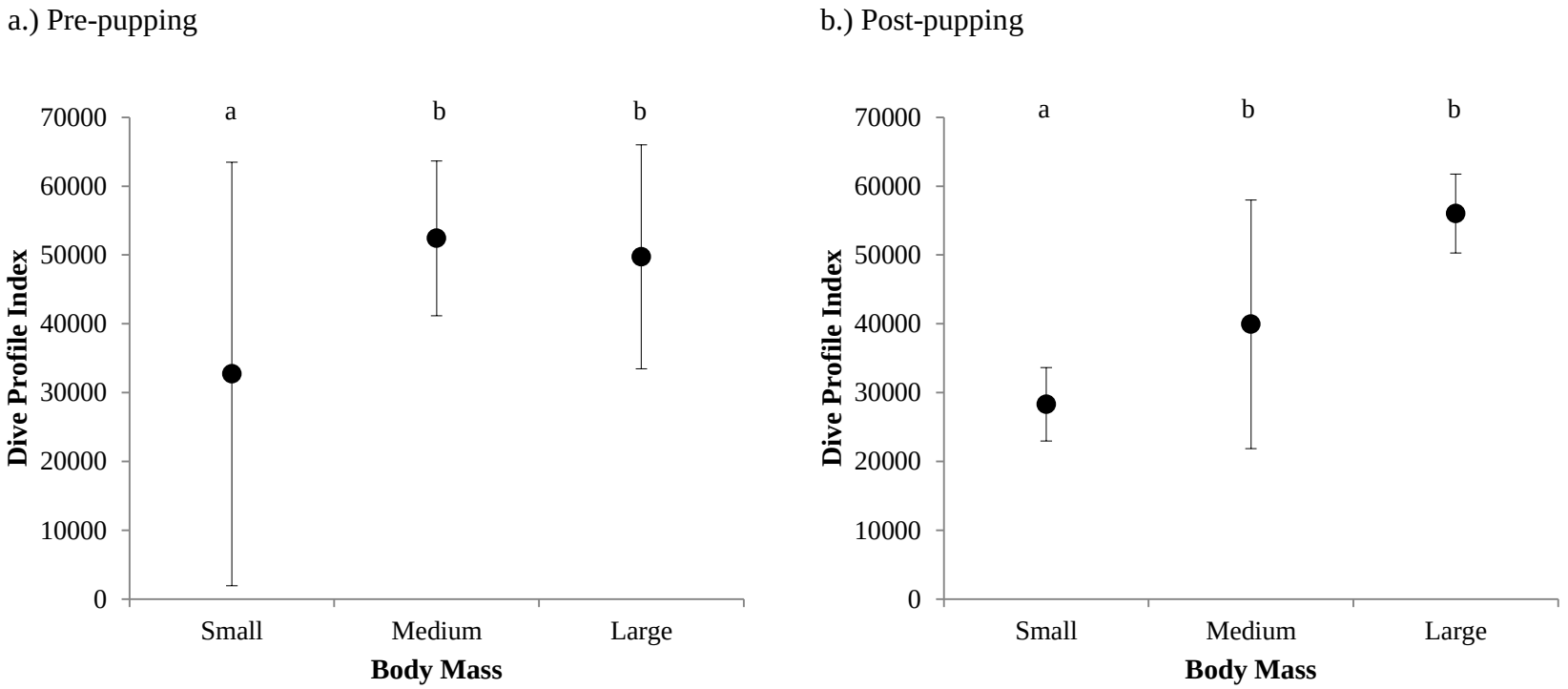
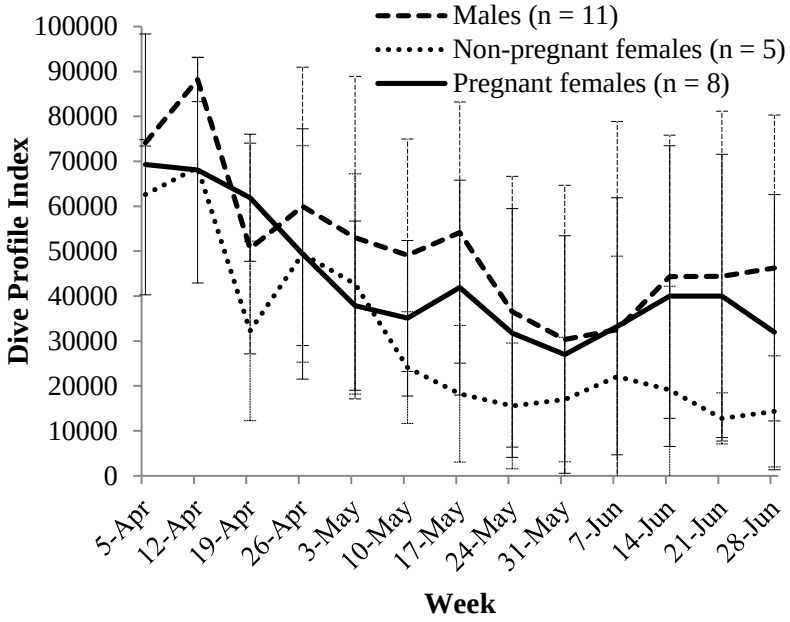


Figure 20. Average total weekly dive profile index by body mass. a.) Pre-pupping season (small significantly less than medium and large, as indicated by a, b, and b, respectively; pairwise t-test with Bonferroni correction; $P < 0.001$ and $P = 0.001$, respectively, no difference between medium and large), b.) Post-pupping season by body mass (small significantly shorter than medium and large, as indicated by a, b, and b, respectively; pairwise t-test with Bonferroni correction; $P < 0.001$ for both comparisons, no difference between medium and large seals). Error bars show standard deviation.

a.) Pre-pupping



b.) Post-pupping

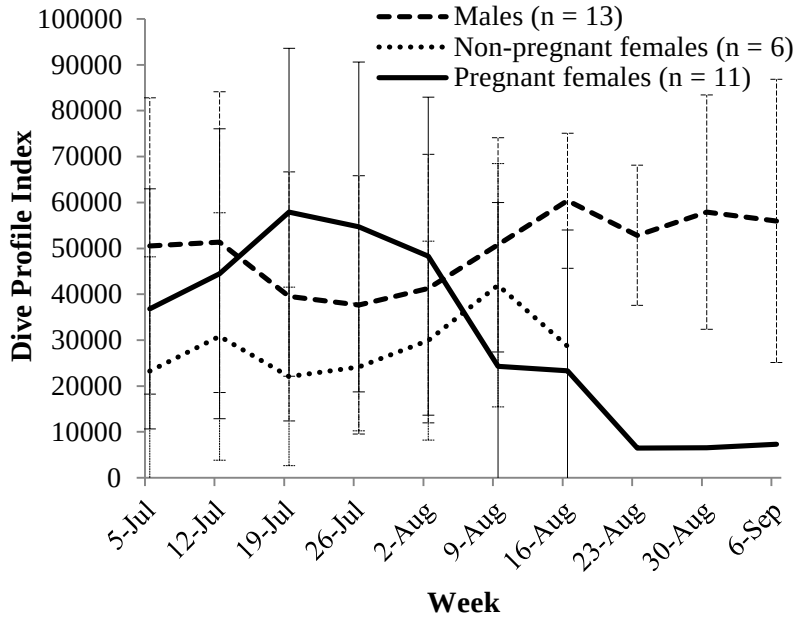
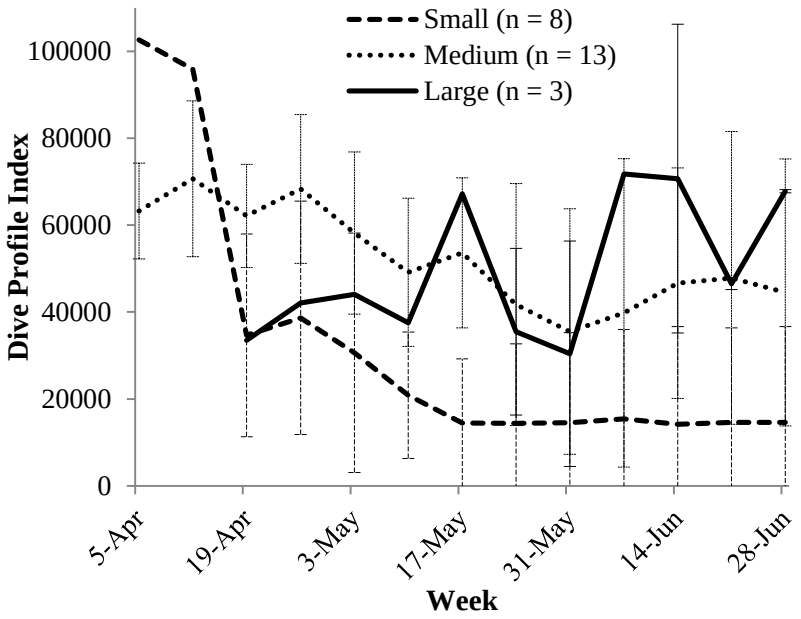


Figure 21. Weekly average dive profile index by sex. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each sex category.

a.) Pre-pupping



b.) Post-pupping

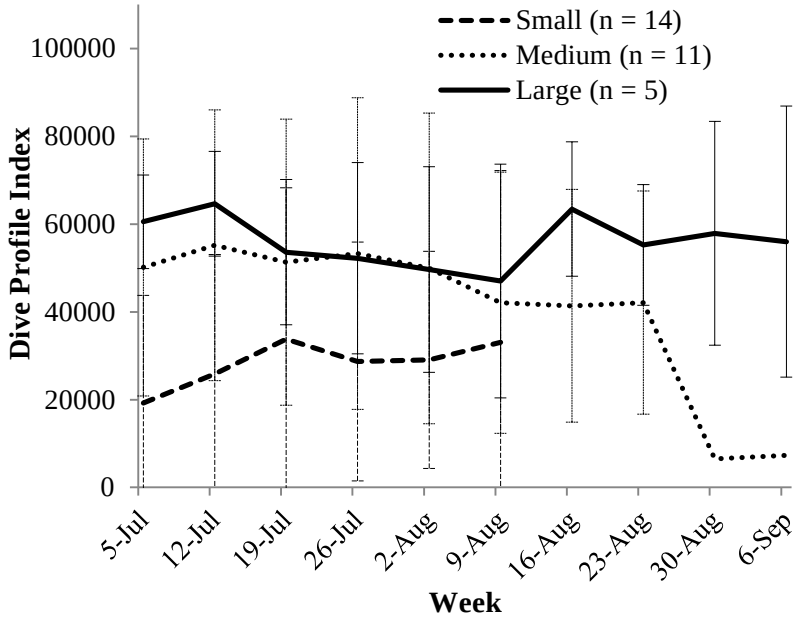


Figure 22. Weekly average dive profile index by body mass. a.) Pre-pupping season, b.) Post-pupping season. Error bars show standard deviation for each body mass category.

Table 12. Results of significant findings (Y = significant, N = not significant) from Linear Mixed Effects Models comparing sex and body mass to weekly average depth, average duration, total number of dives, total number of bouts and DPI for the pre-and post-pupping seasons.

	Depth		Duration		# of Dives		# of Bouts		DPI	
Attribute	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Sex	N	N	N	N	N	N	N	N	N	N
Body mass	**Y**	N	N	**Y**	N	N	N	N	**Y**	**Y**

Discussion

The data on the diving behavior of harbor seals in the inland waters of Washington support the hypothesis that in monomorphic pinnipeds diving behavior, and by extension foraging behavior, is influenced by body mass. In addition the results do not support any of the sex-driven hypotheses. This finding could be due to three factors: 1) that sample size was too small to detect differences, 2) that energetic needs of reproduction do not drive diving behavior, and/or 3) that energetic needs are not significantly different for males and females. Larger males and females behaved similarly to one another, as did smaller males and females. Body mass influenced average maximal depth per week during the pre-pupping season and average weekly dive duration during the post-pupping season: small seals did not dive as deep nor as long as medium or large seals. Body mass also influenced DPI during both the pre- and post-pupping seasons, with small seals having a lower average DPI than medium or large seals. Neither sex nor body mass influenced average number of dives or average number of bouts per week.

The influence of body mass on the foraging time and depth of Washington harbor seals was opposite that of size-dimorphic grey seals and ungulates; whereas foraging

duration of grey seals decreases with increasing body mass (Beck et al. 2003b), dive duration and depth of Washington harbor seals increased with increasing body mass. Increasing dive duration and depth with increasing body mass is consistent with that of cetaceans; as body mass and muscle myoglobin increase, so does dive duration (Noren and Williams 2000). These findings suggest that harbor seals, unlike their size-dimorphic pinnipeds counterparts, do not support the gut-size or prey size hypotheses of efficient foragers. Rather, they support the hypothesis that large animals spend more time foraging. Large animals spent more time foraging perhaps because they are less adept at prey capture, they take more time handling large prey, they need to spend more time foraging to meet their caloric requirements, or because they are able to increase their dive duration by diving to depths that allow them to maximize oxygen use. Elephant seals, also a size-dimorphic species, exhibit similar trends to those of harbor seals, but with a slight sex-body mass interaction. For elephant seals, dive duration increases with body mass in non-pregnant females, though when all sexes are combined, the differences are lost. Pregnant females dive for longer periods than do post-pupping females, a result not observed in this study (Le Boeuf and Laws 1994).

It is clear that body mass influenced dive behavior of harbor seals in this study. It is, however, unclear which factor or factors underlined the observed differences, including prey availability (e.g., its spatial distribution), and energetic needs (e.g., seasonal variation).

Prey availability and diet

Significant effects of body mass on harbor seal dive depth, duration, and DPI were present, with larger animals diving deeper and longer, and having higher DPIs than smaller animals. This difference could be due to prey availability, as has been shown in other studies. For instance, the in-water spatial distribution of harbor seals in San Francisco Bay were most correlated to benthic prey abundance, followed by bottom relief, mid-water prey abundance, depth, and human use (Grigg et al. 2012). Although the results were not reported in terms of vertical distribution, it follows that dive behavior also would be influenced by similar factors. Harbor seals in Washington exhibit patterns by body mass that could be attributed to prey distribution, with large seals potentially targeting benthopelagic and demersal species, and small seals targeting prey that reside in the upper parts of the water column or in shallow inshore waters and estuaries. Larger animals require more energy to survive, thus it follows that nutrient-rich pelagic fish would be the best prey choice compared with smaller estuarine or less nutritionally valuable demersal species. Larger pelagic prey are more difficult to catch, so dive duration would increase to allow for maximum intake of energy-rich prey. Additionally, the sudden presence of a seasonal, high-nutrient prey species in the area (such as pink salmon [*O. gorbuscha*] during odd years) for a few weeks might lead to a significant difference in foraging effort (as seen in DPI results) during that time, compared with non-significant results in DPI earlier in the spring/summer.

Scat sample analyses of San Juan Island harbor seals in 2005–2008 indicated that top prey species included pelagic, benthopelagic, and demersal species (Lance et al. 2012). Specific prey were targeted coincident with their spawning periods. Targeted prey fell into

three groups: adult salmonids, small schooling forage fishes, and non- or loosely-schooling fishes and cephalopods. Pacific herring were the most commonly consumed prey year-round (29% frequency of occurrence [FO] in scats in summer/fall, 39% in winter, and 63% in spring), followed by adult salmonids (51% FO in summer/fall, 9% in winter, and 4% in spring), sand lance (16% FO in summer/fall, 33% in winter, and 25% in spring), anchovy (*Engraulis mordax*; 1% FO in summer/fall, 17% in winter, and 10% in spring), and walleye pollock (12% FO in summer/fall, 8% in winter, and 13% in spring; Lance et al. 2012).

These results contrasted those of seals living on Protection Island (~45 km SW of the San Juan Islands), who did not target adult spawning herring, which one would think would be nutrient-rich (Thomas et al. 2011). During the spawning season, scat sample analyses showed that, of the herring consumed by harbor seals, 74% were juveniles and 26% were adults (Thomas et al. 2011). By contrast, during the post-spawn season, 37% were juveniles, while 63% were adults (Thomas et al. 2011). Juvenile herring school nearshore close to the bottom during the day, and then migrate towards the surface at night. During the pre-pupping season, small seals dived significantly shallower than medium or large seals. These dive depths are consistent with small seals targeting juvenile herring during the pre-spawn season (pre-July 22; Thomas et al. 2011), or targeting all age-groups of herring during nighttime hours when vertical migration brings them to the surface.

The second-most targeted prey in the San Juan Islands were salmonids, particularly during the summer and fall of odd years (2005 and 2007; FO in spring = Lance et al. 2012). During the post-pupping season, larger animals spent significantly more time foraging than did small seals. Coinciding with these changes in foraging duration, fall salmon runs begin

in August and continue until January and February (Laufle et al. 1986, Lassuy 1989). Several species of salmon, including sockeye (*O. nerka*), coho (*O. kisutch*), pink, and Chinook (*O. tshawytscha*), are found in marine waters of Washington (Beauchamp et al. 1983, Laufle et al. 1986, Lassuy 1989). Sockeye, coho, and pink salmon run in the fall (Laufle et al. 1986, Bonar et al. 1989, Lassuy 1989), whereas Chinook run in three groups (spring, summer, and fall) and, hence, are present in waves throughout both seasons (Beauchamp et al. 1983).

Consistent with the timing of fall salmon runs, salmonids make up a large portion of the diets of harbor seals in Washington during the summer months, and large seals dive for significantly longer periods than small seals (London 2006, Lance et al. 2012, Luxa and Acevedo-Gutiérrez 2013). Salmonids present more of a challenge to hunt than herring, as they are bigger and do not school as tightly as herring. Consequently, they may require more foraging time for successful feeding events (Simon et al. 2007). Larger seals may have to forage for longer periods of time to successfully land metabolically required amounts of the fish. Additionally, handling time of prey increases with size, and because larger animals are able to eat larger prey, they may increase dive duration as a result of increasing handling time (Cohen et al. 1993).

The third most preyed upon fish was walleye pollock (15%), followed by threespine stickleback (*Gasterosteus aculeatus*; 12%), rockfish spp. (12%), shiner perch (*Cymatogaster aggregata*; 11%), cephalopods (11%), and Pacific sand lance (10%; Lance and Jeffries 2007, Lance et al. 2012). Analyses of scats collected from various points in Hood Canal during 1998-2000 showed Pacific hake as top prey (80%), followed by Pacific herring

(45%), salmonids (26%), and shiner perch (10%; London et al. 2002). Padilla Bay scat sample analyses showed gunnels (family Pholidae; 89%), snake prickleback (*Lumpenus sagittal*; 59%), Pacific staghorn sculpin (*Leptocottus armatus;* 50%), shiner perch (48%), and threespine stickleback (18%) as top prey items for harbor seals (Luxa and Acevedo-Gutiérrez 2013).

Analysis of fatty acids revealed that there were significant differences in diets by sex and by haul-out site in the harbor seals studied for this project (Bromaghin et al. 2013). Seals at Bird Rocks and the Belle Chain Islets in British Columbia showed the highest diversity in their diets. The most common prey for those two haul-out sites were black and yellowtail rockfish, salmonids, Pacific herring, shiner perch, and spiny dogfish (*Squalus acanthias*; Bromaghin et al. 2013). Padilla Bay seals ate predominantly shiner perch. Comparisons by sex revealed that females consumed predominantly shiner perch, whereas males consumed black and yellowtail rockfish, Pacific herring, and spiny dogfish (Bromaghin et al. 2013). Rockfish composed greater than 10% of the diet of harbor seals in the Salish Sea, a finding that was not consistent with scat sample analyses, suggesting that seals do not consume the hard parts of rockfish (Lance et al. 2012, Bromaghin et al. 2013).

Capture data show that eight of the seals captured in Padilla Bay were categorized as "small" seals, so the food habits results are consistent with the dive behavior results (small seals did not dive as deep or for as long). Juvenile herring and other small prey have a lower handling time than larger prey, so it is possible that small seals monopolize on the easy-to-catch prey. Demographics of Padilla Bay, if not prey-driven, could also be due to haphazard capture techniques (the smallest seals had the least life experience and therefore were the

ones caught in the net), increased maneuverability for smaller, more agile seals in shallow waters and on the mudflats, ease of prey capture for small animals (both because there are higher concentrations of benthic prey in the estuary and because they are in shallow waters), reduced competition with larger animals at potentially more favorable haul-outs (e.g., Bird Rocks, where access to herring and salmonids may be greater), and protection from transient killer whales (*Orcinus orca*), which may be less likely to prey on seals in very shallow waters.

One other factor that affects pinniped diving patterns is vertical distribution of prey, diurnal or otherwise. Many planktivorous pelagic fish, including herring and sockeye salmon, perform diurnal vertical migrations, following zooplankton deep by day and shallow by night (Blaxter and Parrish 1965, Clark and Levy 1988). Although Thomas et al. (2011) did not see harbor seal dive behavior reflect vertical distribution of herring, Reuland (2008) did see diel patterns in diving. Female fur seal foraging behavior has been shown to be influenced by sea surface temperature and duration of night (McCafferty et al. 1998). 55% of dives occurred at night, though diel patterns, as well as trends in dive depth, likely were due to location of krill in the water column (McCafferty et al. 1998). Southern elephant seals' dive depth also was strongly correlated to the light intensity at 150 m, which could be attributed to prey vertical distribution and maximizing foraging efficiency (Jaud et al. 2012). Of the variance in dive depth, 60% was explained by light attenuation at 150 m. Light attenuation and temperature influence where the prey are distributed in the water column, which in turn determines depths to which southern elephant seals dive (Jaud et al. 2012).

Coupling the results of the fatty acid analyses of harbor seal diet with dive data for each individual in this study may reveal whether dive behavior can be used as a proxy for dietary choices. It would be particularly interesting to compare dive data of the individuals that preyed predominantly on black and yellowtail rockfish, versus those which showed no indication of preying on rockfish. Heterogeneity between males and females in the fatty acid results could be due to differing energetic needs because of costs of reproduction, reduced intersexual competition for food, or other factors, but comparing diet data with dive data could help explain these differences.

Spatial distribution

Spatial distribution may play a role in dive behavior, as different available habitats and water depths will be limiting factors for dive depths and durations. Haul-out sites in Padilla Bay are only available at high tide, so by default seals would be required to enter the water with the incoming tide. Seals could then begin bouts of diving. Because all sizes of seals were tagged in Padilla Bay, all sizes would enter the water as the tide flooded, hence there were no significant differences by body mass. Additionally, it is noteworthy that harbor seals in Padilla Bay could be bottom resting once their haul-out is unavailable, a behavior in which the seals sleep on the bottom, which could be masked as dives or dive bouts.

In this study, size and locally-available depths were potentially confounded. Eight small seals, three medium seals, and one large seal were captured in Padilla Bay, whereas only medium and large seals were captured at the Bird Rocks site, so, although the model

did not show a site effect, habitat immediately available to the seals is consistent with the dive depths shown by each size category. Four small, seven medium, and seven large seals were captured in Hood Canal, revealing a more even size distribution.

Although there were no significant differences by sex, it is possible that low sample size masked any effects of sex. Results from Peterson et al. (2012; who used data from a sample of the animals used in this study) suggest that with a higher sample size for her study, spatial movement may be influenced by sex. They tracked 16 male and four female harbor seals in the inland waters of Washington, and determined that they moved further than normally documented for the species (Peterson et al. 2012). Typical movement is <50 km from their primary haul-out, but eight of the males traveled >100 km, with two of those moving >400 km. The farthest that a female traveled was 41.6 km (Peterson et al. 2012).

Peterson et al. (2012)'s results are consistent with those of Harvey et al. (2012) and Breed et al. (2009), both of whom studied sex-specific spatial movement of grey seals. Male and female grey seals forage in different areas in the Gulf of St. Lawrence and the Scotian Shelf ecosystem (Breed et al. 2009, Harvey et al. 2012). Males fed in areas of high prey density, whereas females fed in areas of low prey density. It should be noted, however, that grey seals are a size-dimorphic species, therefore differences could be due to body mass rather than sex.

Given the results of my study, investigating spatial movement by body mass may show similar trends. It is hypothesized that perhaps the males were moving to where estrus females were, on the outer coast, so perhaps their diving behavior would also coincide with that of females during the breeding season. Spatial movement could be a factor involved in

diving behavior, thus it would be interesting to compare dive patterns with spatial movement with a greater sample size.

Energetics and diving physiology

Basal metabolism, locomotion, reproductive season and prey digestion are all factors that contribute to energy expenditure and energetic needs in seals (Williams et al. 2004). Although we did not investigate energy intake and use in this study, evidence from other studies suggests that large animals with higher energetic needs dive deep to conserve energy, and to maximize dive time, prey capture and foraging efficiency (Hill et al. 1987, Williams et al. 2000). Results of analysis of dive depth, duration, and DPI in this study may support this evidence.

In grey and harbor seals, body condition parallels reproductive season, with males having the most mass leading up to the breeding season, then losing it during the breeding season, when mate acquisition is their main focus rather than foraging (Walker et al. 1993, Beck et al. 2003a). Females are heaviest in the spring, during the final stages of gestation, the pupping season, and the nursing season. Body condition is also correlated with prey choice, and diet differences paralleled differences in diving patterns (Beck et al. 2007). Because grey seals are size-dimorphic, it is possible that differences are mass-related rather than sex-related (Beck et al. 2007). Thus, larger animals would exhibit greater foraging effort, such as is demonstrated by DPI.

Harding et al. (2005) showed that, compared to larger pups, small harbor seal pups have higher energetic needs to maintain thermoregulation during the cold part of the year in

the northern Skaggerak, Sweden. A 17 kg pup, for instance, began to expend energy on thermoregulation two to three months earlier than a 32-kg pup. In order to keep warm in the coldest time of year, a 32 kg pup needed to eat an extra 0.4–0.5 kg of fish, compared to 0.9–1.0 kg for a 17 kg pup (Harding et al. 2005). Maintaining optimal body condition (enough blubber to keep warm without causing excess energy expenditure on locomotion) is essential through the winter for thermoregulatory, reproductive, and energy efficiency reasons.

Marine mammals have physiological adaptations to aid in optimizing energy use that, with more research, could be found to contribute to dive differences in the seals in this study. The mammalian dive reflex is an energy-saving mechanism that is maximized by diving deep. The reflex is activated when a mammal's face contacts cold water, but is greatest when the animal dives to high pressures and is not actively stroking (Davis and Williams 2012). It induces bradycardia, body temperature decrease, and peripheral vasoconstriction, thus lowering the metabolism and conserving energy (Hill et al. 1987). Also, as mammals dive, air spaces are compressed, decreasing the volume of the animal without decreasing the mass (Williams et al. 2000). This volume decrease reduces the buoyancy of the animal. At the point when the force of drag on the animal is less than the buoyancy, the animal can begin to glide, rather than constantly stroking as is necessary (and energetically inefficient) at shallower depths (Williams et al. 2000, Davis and Williams 2012). Thus, deep diving is more efficient than shallow diving. Marine mammals also have maximal oxygen storing capabilities because they have a large blood volume, and they have high concentrations of hemoglobin in their blood and myoglobin in their muscles (Kooyman

2002). It follows, then, that larger animals have larger availability for oxygen stores, and therefore can dive deeper and for longer.

Increased oxygen storage is advantageous both for feeding purposes, as it allows more extensive foraging, but also for breeding. Having larger energy stores going into the mating season allows for foraging effort to be diminished during it, thereby allowing males to focus more time and energy on mate acquisition (Coltman et al. 1998). Consistent with the findings in this study, body mass was a major factor influencing the bioenergetics model for SJI harbor seals (Howard et al. 2013). Body mass and metabolic rates coincide closely, so it follows that behaviors driven by energetic needs (i.e., diving) would also be influenced by body mass. During non-breeding seasons, reproductive factors (lactation and digestion) were not major factors in the model. During the breeding season, however, removal of reproductive factors from the model resulted in a 10% decrease of estimated energetic needs (Howard et al. 2013). Given these findings, perhaps with a larger sample size in the present study, an influence of sex on diving behavior would have been detected in this study.

Potential influences of season

Energetic needs vary by season (e.g., reproductive status/period and the molt), and it was surprising that reproductive status (represented by comparisons by sex) did not play a significant role in diving behavior. Differences in DPI were detected by body mass during both the pre- and post-pupping seasons, and in dive depth and duration in the pre- and post-pupping seasons, respectively.

In early spring, herring are abundant as they move inshore to spawn in estuaries and bays surrounding the San Juan Islands, Padilla Bay, and Hood Canal, gathering near spawning grounds several weeks before spawning (Lassuy 1989). During the summer, there is a shift in prey choice by seals from herring to salmon (London 2006, Lance et al. 2012, Luxa and Acevedo-Gutiérrez 2013), an epipelagic species that lives within the top 30 m of the water column (Quinn 2005). It is likely that all sizes of harbor seals shift their diet to target salmonids during their migration, which explains the lack of significant difference in dive depth in the post-pupping season.

Another factor to consider is that dives have many purposes, including foraging, traveling, energy conservation, and digestion, and proportions of each can change without affecting individual dive variables (Baechler et al. 2002). Although dive shapes do not fully represent specific functions of dives, they can demonstrate potential differences in dive purpose (Baechler et al. 2002). Differences in proportion of U- (presumed foraging) versus V-shaped dives have been noted in North Atlantic harbor seals by sex and season. Based on identification of dive types, lactating females show a 9-fold increase in foraging dives from early to late lactation, and males' foraging dives decrease from 63% of total dives to only 45% between pre-breeding and breeding seasons (Baechler et al. 2002). Male harbor seals in the same region did not alter their dive durations between pre-breeding and breeding, but instead the durations were spent loitering in the waters surrounding the haul-out where they were more likely to encounter females in estrus (Coltman et al. 1998). These differences were not examined by body mass, though trends by body mass may also exist. Although we

do not see differences in number of dives, there could be significant differences and temporal changes in proportion of dives with certain purposes by sex and/or body mass.

Methodology

Studies of marine mammal and bird diving behavior typically investigate behavior on a focused scale by classifying and analyzing individual dives (e.g., Lesage et al. 1999, Beck et al. 2003a, Thomton et al. 2008). This study approached harbor seal diving behavior from a broader scale by summarizing behavior over 1-week periods. This approach minimized autocorrelation while maintaining data variability. I also included two variables that are not presented in the literature: number of bouts per week and DPI. The others, dive depth, duration, and some measure of frequency of dives (e.g., number of dives/h), are factors that typically are included in focused analyses for determining dive shape or for making individual comparisons.

The Dive-profile Index provides a summative datum that represents an integrative snapshot of a seal's dive profile. This analysis method provides a new and useful way to compare animals' diving behavior without losing valuable information. DPI uses the visual 2-dimensional representation of dive depth, duration, number of dives, and number of bouts to explain one variable, rather than single-dimensional numbers as are usually used in these types of analyses. Although "one DPI unit" has not yet been defined, definition of one unit will aid in comparison across studies. DPI can be useful to analyze a summary variable that combines many aspects of diving behavior. As a measure of "dive effort," Hiruki-Raring et al. (2012) defined dive intensity by summing all the depths and also all the durations of

seals' dives for a pre-defined period, then dividing by the number of days in that period. Coupled with daily prey abundance surveys, this method of determining dive effort allowed for comparing trends in diving with prey availability per day. DPI is another way of defining "dive effort." Hiruki-Raring et al. (2012)'s method could also be used with DPI, but comparing prey by week, or calculating DPI by day.

By averaging data weekly, I was able to discuss diving behavior on a broader-scale than would have been possible by analyzing each individual dive or bout, and I also minimized loss of variability from averaging. I was able to determine which animals are likely to encounter prey at different depths in the water column, and which animals likely impact prey populations by spending longer durations foraging. Individual dives, the percentage of dive types included in general diving behavior, and breakdowns of individual dives (i.e., ascent rate, descent rate, and bottom time) are informative when investigating factors including activity budgets, and time spent foraging versus resting versus traveling. They also are informative for answering questions about energetics of movement. When looking at general diving behavior, however, averaging variables by week shows a broader picture of a seal's life and preferences. Additionally, when comparing effects on an ecosystem by sex or body mass, for instance, general variables, such as weekly averages are easier to compare temporally with prey and/or environmental data, and by sex or body mass than each dive individually.

Biological Relevance and Impacts on Prey Populations

In the Pacific Northwest, body mass explained differences in diving behavior of monomorphic harbor seals, whereas sex did not. The results of this study support two body mass hypotheses: that larger seals exploit more space and that larger seals utilize longer foraging times. By diving to optimal depths for energy efficiency, large seals are able to spend more time foraging. Likewise, large seals have more oxygen storing capacities and potentially spend more time foraging as a result.

The inland waters of Washington provide habitats for many different species of fish, and the flux of prey throughout the year allows for a variety of dietary choices for opportunistic predators such as harbor seals. As a result, diving behavior fluctuates, coincident with prey changes. Several fish species in these waters are showing depressed numbers, including rockfish, herring, and salmonids (West 1997, Gaydos and Brown 2009). Rockfish are the most depressed, and although analysis of hard parts in scats do not show these fishes to compose a large portion of harbor seal diet, fatty acid analysis revealed that, in some individuals, they compose up to 50% of the diets (Bromaghin et al. 2013). With population numbers already low, and seal numbers high, even small amounts of predation by individual seals could have devastating impact on recovery of rockfish stocks (Bromaghin et al. 2013).

Of equal concern is the impact that harbor seals have on their dominant prey species: Pacific herring and Pacific salmonids. Seasonal shifts in prey preference (e.g., from herring to salmon, or from many less abundant species to one abundant species) likely account for seasonal differences in diving behavior between groups. During the winter, harbor seals

have a diverse diet largely composed of Pacific herring, walleye pollock, shiner perch, rockfish species, and sculpins (Lance et al. 2012). During the spring and summer, scat sample analysis shows that prey preference shifts from the diverse diet to 80% frequency of occurrence of Pacific herring, then to 80% frequency of occurrence of salmonids, respectively (Lance and Jeffries 2007). Scat analyses show that harbor seals disperse their foraging efforts across different species during different seasons. Dive data add a body mass component to the scat analyses results by showing that large animals may be the individuals targeting, and thus potentially stressing, deeper-dwelling species, whereas smaller animals may be targeting shallower-dwelling species.

Herring consumption estimates for the harbor seal population in the San Juan Islands and Eastern Bays are 646 ± 303 Metric Tonnes during the pre-pupping season and 2,151 ± 706 MT during the post-pupping season, for a total of 2,797 ± 1,009 MT per spring/summer (Howard 2009). The overall US commercial catch for Pacific herring in 2009 was 40,244 MT (Van Voorhees et al. 2010). Of that number, 39,474 MT were caught in Alaska, so the difference of 770 MT was caught in United States Pacific waters outside of Alaska. San Juan Island harbor seals, then, eat over 3.5 times the non-Alaska US commercial catch. This number does not account for predation in Puget Sound and Hood Canal, so is likely an underestimation. These predation numbers are sure to impact herring populations in the area.

During the post-pupping season, there was no difference in dive depth. Given that all sizes of harbor seals are foraging at the same depth, it follows that large and small seals likely target the same prey in the summer months. Large animals spend more time foraging and have higher DPIs, indicating that they have a larger impact on a given prey species.

During the post-pupping season, salmonids move into the area to begin traveling up rivers to their spawning grounds. These species are abundant and nutritious, thus are a favorite of harbor seals (Lance and Jeffries 2007). San Juan Island harbor seals are estimated to eat 783 ± 380 MT of salmonids during the pre-pupping season and 675 ± 388 MT during the post-pupping season, for a total of 1,458 ± 768 MT/year (Howard 2009). US (including Alaska) commercial catch statistics recorded a total of 319,878 MT caught in 2009 (Van Voorhees et al. 2010). Washington's salmon catch for 2009 was 14,338 MT (Van Voorhees et al. 2010). Harbor seals, then, eat the equivalent of 10% of the total commercial salmon catch in Washington. ~1,500 MT is not an insignificant quantity of salmonids; therefore harbor seals likely impact their populations. Because the significant influence of body mass on dive duration (large seals spend more time diving than smaller seals) was only present during the post-pupping season, when salmon are also abundant, the influence of large seals on salmon may be greater than that of small seals.

Understanding the diving behavior of marine mammals by sex and by body mass throughout the year can help us determine which size and sex classes of seals have the greatest impact on prey populations during times when different prey is present. Comparison of diving behavior and fatty acid analysis will help us determine if diving behavior can be used as a proxy to prey choice, which would expand the possibilities for dive behavior aiding in management. Also, comparing spatial use to diving behavior by body mass and by sex can reveal how animals from different regions use their habitat, and how broad that habitat is. Animals that spend more time foraging or have larger DPIs are more likely to reduce prey numbers. Animals that dive to shallower depths do not target deep-dwelling

prey species, and thus, are not responsible for decline of those species. Ecosystem-based management, as outlined in Kershner et al. (2011) is being practiced in Puget Sound, but contributions to dietary niche based on dive behavior could aid in better understanding the role of harbor seals in this method of management. This information is useful in making management decisions regarding conservation of both the individual species, both prey and predator, and the ecosystem as a whole. Such decisions may include a need to cull harbor seal populations that are targeting depleted fish stocks, or implementation of Marine Reserves and Marine Protected Areas accounting for proximity to harbor seal haul outs. Investigating diving patterns can be a useful aid in determining if and how predators are depleting or inhibiting recovery of depressed prey stocks.

Conclusions

Anthropogenic and other stresses are increasing in our oceans' ecosystems. Fish stocks are increasingly depressed, and the complex causes of such depressions are not completely understood. Investigating declines in fish stocks from an ecosystem-wide perspective can help more thoroughly inform management decisions. Although marine mammals and other top predators have not been implicated in the actual decline of fish stocks, they have been noted as a possible cause of stunted recovery of numbers (Fu et al. 2001, Hansen et al. 2006, Trzcinski et al. 2006). By determining the amount of time spent foraging, and spatial and vertical movement of predators and location of prey, understanding diving behavior can help inform management about potential negative impacts of different groups of marine predators.

Diving behavior is a broad term classified by combining many different factors of diving. For this study, I defined "diving behavior" using five variables which generalized a week of diving in a harbor seal. Dive depth, dive duration, and DPI proved to be the most informative variables. This study demonstrated that aspects of diving are significantly different by body mass. The differences could account for their energetic needs or be a reflection of preferred prey for the season. Larger seals apparently conserve energy and thus minimize caloric needs by diving deep when optimal prey are available at deeper depths.

Harbor seals in the inland waters of Washington may cause a decline in prey population numbers and/or inhibit depressed stocks from rebounding (Howard 2009). Given the lack of natural predators of the harbor seals in the inland waters, it is possible that human-moderated management will be a necessity in the future, as it was in the past.

One more anthropogenic factor to consider that may impact distribution of harbor seals in Washington is ocean noise. Specifically, marine mammals face impacts of masking due to increased ocean noise (Wartzok 2010), which could cause dispersal of the inland waters of Washington population of harbor seals. Marine mammals can hear sounds between 10 Hz (baleen whales) and 200 kHz (river dolphins), which encompasses the range of most human activities (Wartzok 2010). In the last 40 years, noise in the 20-80 Hz range has increased ~12 dB, largely due to shipping noise (Wartzok 2010). Shipping traffic is expected to increase (Wartzok 2010), which could affect the harbor seals in this study, most of which likely spend some portion of their lives (e.g., foraging, traveling to breeding grounds) in or near shipping lanes (in Puget Sound, the Strait of Juan de Fuca, or Rosario Strait). Although marine mammals are able to vary the frequency and volume of their own communications,

they cannot adjust the frequency and volume of schools of fish or of predators (Wartzok 2010). Hence, masking effects of shipping traffic could impact foraging success and defense mechanisms, causing a shift in habitat use by harbor seals in the inland waters of Washington. This study may serve to provide baseline data on seal diving behavior, allowing for comparison of pre-elevated shipping data to post-elevated shipping data, and, in the event that culling measures are considered, may be useful to determine which animals contribute the most to the depletion of fish stocks.

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Appendix A: Complete harbor seal capture data

Tagging Location
BR = Bird Rocks
HC = Hood Canal
PB = Padilla Bay

Sex
M = Male
PF = Pregnant female
NPF = Non-pregnant female

Size
S = Small (47.0–69.4 kg)
M = Medium (69.5–91.4 kg)
L = Large (91.5–113.5 kg)

Seal ID	Tagging location	Capture Season/ Year	Deployment date	Deployment end	Sex	Size (by body mass)	Length (cm)	Body mass (kg)
B1695	BR	Spr '07	4/4/2007	9/4/2007	M	M	140	71.5
B1696	BR	Spr '07	4/5/2007	8/15/2007	M	M	149	74.5
B1742	BR	F/W '07–'08	11/19/2007	12/22/2007	M	M	163	83
B1744	BR	F/W '07–'08	11/20/2007	2/22/2008	M	M	153	81.5
B1745	BR	F/W '07–'08	1/16/2008	3/28/2008	M	M	147.5	83
B1700	BR	Spr '07	4/19/2007	6/11/2007	M	L	158	110.5
Y1513	BR	F/W '07–'08	1/30/2008	7/3/2008	NPF	M	150	75.5
Y1455	BR	Spr '07	4/4/2007	7/20/2007	PF	M	147	76.5
Y1514	BR	F/W '07–'08	2/25/2008	8/26/2008	PF	M	138	70.5
hc02804	HC	Sum '02	8/28/2002	9/21/2002	M	S	139	61
hc02524	HC	Sum '02	7/24/2002	10/15/2002	M	M	151	80
hc02544	HC	Sum '02	7/24/2002	10/13/2002	M	M	160	91
hc02564	HC	Sum '02	7/24/2002	9/24/2002	M	M	154	83
hc02644	HC	Sum '02	8/6/2002	10/13/2002	M	M	138	78
hc02664	HC	Sum '02	7/23/2002	9/4/2002	M	M	150.5	77.5
hc02505	HC	Sum '02	8/7/2002	10/16/2002	M	L	151	109
hc02704	HC	Sum '02	8/6/2002	11/10/2002	M	L	161	105
hc02724	HC	Sum '02	7/24/2002	10/30/2002	M	L	152	113.5
hc05666	HC	Sum '05	8/24/2005	9/25/2005	M	L	149	103.75
hc02625	HC	Sum '02	8/6/2002	9/1/2002	NPF	S	142	66
hc05487	HC	Sum '05	8/23/2005	9/29/2005	NPF	S	140	60.5
hc05345	HC	Sum '05	8/24/2005	9/19/2005	PF	S	125	49.25
hc05685	HC	Sum '05	8/23/2005	9/23/2005	PF	S	124	48.25
hc05706	HC	Sum '05	8/23/2005	9/24/2005	PF	S	140	49.5
hc02583	HC	Sum '02	8/6/2002	9/17/2002	PF	M	136	82
hc02683	HC	Sum '02	7/25/2002	9/25/2002	PF	M	128	83
B1699	PB	Spr '07	4/18/2007	8/16/2007	M	S	142	64.0
B1712	PB	Spr '07	5/21/2007	8/5/2007	M	S	146	69.0

B1713	PB	Spr '07	5/21/2007	8/28/2007	M	S	135	54.0
Y1456	PB	Spr '07	4/17/2007	7/20/2007	NPF	S	139	55.5
Y1457	PB	Spr '07	4/17/2007	7/25/2007	NPF	S	131	57.5
Y1458	PB	Spr '07	4/17/2007	8/14/2007	NPF	S	128	48.5
Y1459a	PB	Spr '07	4/19/2007	8/24/2007	NPF	M	141	83.0
Y1459b	PB	F/W '07–'08	2/25/2008	8/9/2008	PF	S	132	64
Y1460	PB	Spr '07	4/19/2007	8/6/2007	PF	S	127	62.5
Y1462	PB	Spr '07	5/21/2007	8/23/2007	PF	M	143	77.5
Y1469	PB	Spr '07	5/21/2007	10/6/2007	PF	M	145	85.0
Y1465	PB	Spr '07	5/21/2007	9/11/2007	PF	L	154	103.0